COMPARISONS OF ARCTIC COD, ARCTIC STAGHORN SCULPIN, AND SHORTHORN SCULPIN DIETS THROUGHOUT THE NORTHEASTERN CHUKCHI AND WESTERN BEAUFORT SEAS

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A

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Abstract

Diet information for Arctic Cod (*Boreogadus saida*), Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), and Shorthorn Sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort seas is mostly descriptive. In this study, I examined diet variability due to region, depth, and body size by quantitatively comparing these fishes' diet compositions. To accomplish this, I analyzed the stomach contents of 1,620 fishes collected over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011). In general, body size and region accounted for most differences in diets. As body size increased, each species consumed a more varied diet composed of larger prey. Additionally, each species consumed more benthic prey taxa in the northeastern Chukchi Sea than in the western Beaufort Sea. These findings indicate that a combination of both body size and region-specific oceanographic processes are likely driving the observed variability in these species' diets. Documenting this variability provides a better insight into the present relationships between these fishes and their prey over a large area and offers a benchmark for future diet analyses in the western Arctic.

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Introduction

Fishes are important links between lower and higher trophic level organisms in Arctic marine food webs (Lowry and Frost 1981; Bradstreet and Cross 1982; Craig et al. 1982; Atkinson and Percy 1992), yet knowledge of their diets is limited (Mecklenburg et al. 2008). Arctic Cod (*Boreogadus saida*), Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), and Shorthorn Sculpin (*Myoxocephalus scorpius*) are members of the two most abundant fish families in the western Arctic: Gadidae (cods), and Cottidae (sculpins; Barber et al. 1997; Norcross et al. 2013). In the past 15 years, there has been little published data on these fishes' diets in the northeastern Chukchi Sea (hereafter, Chukchi Sea) and western Beaufort Sea (hereafter, Beaufort Sea). Of the available studies, most differ in design, are regionally isolated, small in sample size, and as a result they lack the quantitative detail needed to accurately model food web dynamics (Whitehouse 2013). Therefore, updating this information would enhance current U.S. western Arctic food web models. Additionally, because issues such as climate change (Renaud et al. 2012) and resource development (Sturdevant et al. 1996) could alter present relationships for fishes and their prey in the Arctic, the information gained from my research could serve as a benchmark to compare against future changes. I address these issues by comprehensively comparing the diet compositions of Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin collected from the Chukchi and Beaufort Seas.

Studying both cod and sculpins allows for a wide view of Arctic fish food habits because Arctic Cod generally inhabit different parts of the water column than Arctic Staghorn Sculpin and Shorthorn Sculpin and each consume different prey types throughout their ranges. Arctic Cod is primarily regarded as an open-water, pelagic, ice-associated forage fish (Lønne and Gulliksen 1989), although it is found throughout the water column in ice-free areas as well

(Walkusz et al. 2011; Norcross et al. 2013). This fish is typically a pelagic predator (Lowry and Frost 1981; Lacho 1986) that feeds on calanoid copepods, ice-associated amphipods, hyperiid amphipods, euphausiids, and other fishes (Lowry and Frost 1981; Craig et al. 1982; Coyle et al. 1997; Rand et al. 2013). Its food habits are flexible, allowing Arctic Cod inhabiting shallower regions (Bluhm and Gradinger 2008) to feed on bottom-associated (benthic) prey such as benthic amphipods and cumaceans (Coyle et al. 1997; Cui et al. 2012). In contrast, Arctic Staghorn Sculpin and Shorthorn Sculpin diets appear less flexible; both are chiefly benthic feeders (Moore and Moore 1974; Atkinson and Percy 1992; Coyle et al. 1997; Cui et al. 2012). In general, Arctic Staghorn Sculpin consumes benthic and epibenthic prey, including benthic amphipods, bivalves, cumaceans, and polychaetes (Atkinson and Percy 1992; Coyle et al. 1997). There is no published diet information for Shorthorn Sculpin in the Chukchi and Beaufort Seas; however, this species is known to consume mainly benthic crustaceans, decapods, fishes, and polychaetes throughout its Arctic distribution (Moore and Moore 1974; Atkinson and Percy 1992, Cardinale 2000; Cui et al. 2012). Because both sculpins mainly inhabit the benthos, I expect their diet compositions to be more similar to one another than to that of Arctic Cod.

Of great interest to my research is whether habitat (i.e., sea, sea-region, or depth category) and fish body size affect the diets of Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin. Both factors are known to create diet variability (Scharf et al. 2000; Renaud et al. 2012) but are largely unaccounted for in previous accounts of these fishes' diets. Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin diets likely differ between the Chukchi and Beaufort Seas due to differences in biological productivity, prey compositions, and physical oceanography. Regions of the highly productive and shallow Chukchi Sea shelf (Weingartner 1997; Weingartner et al. 2013) are characterized by favorable, current-driven carbon deposition

that supports a predominantly benthic food web (Grebmeier et al. 2006; Blanchard et al. 2013). In contrast, the narrower shelf of the Beaufort Sea receives less nutrient-rich subsidies, and is characterized as less locally productive in terms of both primary (Belkin et al. 2009) and secondary benthic productivity (Carey 1991). These broad-scale differences should be reflected in diet compositions, with each species in the Chukchi Sea potentially consuming proportionally more benthic prey than Beaufort Sea conspecifics. Similarly, each species' body size is expected to create diet variation because as fishes grow larger, they become more proficient at eating larger, more profitable prey (Werner and Hall 1974). This ontogenetic shift in prey use is documented in Arctic Cod populations throughout the Arctic (Lowry and Frost 1981; Craig et al. 1982; Bradstreet et al. 1986; Jensen et al. 1991) but not documented in Arctic Staghorn Sculpin and Shorthorn Sculpin diet studies. I expect that prey diversity and prey size will increase with increasing body size for both sculpin species, similar to what is described for the confamilial Longhorn Sculpin (*Myoxocephalus octodecemspinosus*), found along the northeast U.S. coast (Scharf et al. 2000).

Stomach contents analysis, i.e., the dissection of fish stomachs and identification of resulting prey items, forms the base of my diet comparison study. I chose this method because it is useful in understanding trophic linkages within natural ecosystems (Pinnegar et al. 2003) and because it offers greater taxonomic resolution than other methods, including analysis of stable isotopes or fatty acids (Kolts et al. 2013). Fish diet compositions can be quantified in many ways (Hyslop 1980; Baker et al. 2013). I use a combination of gravimetric, numeric, and occurrence-based calculations along with univariate and multivariate statistical methods to show similarities and differences in each species' diets throughout the Chukchi and Beaufort Seas.

The focus of my first chapter was to compare Arctic Cod diet composition within and between the Chukchi and Beaufort Seas by size classes. I hypothesized that Arctic Cod diet would differ within seas with changes in fish body size, and between seas due to the inherently different biotic and abiotic processes characteristic of the Chukchi and Beaufort Seas. While diet data exist for Arctic Cod in both seas, there is no formal comparison between the Chukchi and Beaufort Seas. A comparison such as this increases our understanding of Arctic Cod diet variability, the results of which could increase our knowledge of this ecologically important species and provide better data for food web models.

In my second chapter, I compared Arctic Staghorn Sculpin and Shorthorn Sculpin diets within habitats of interest in the Chukchi and Beaufort Seas. These habitats included four regions and two depth levels within each sea. I structured the study this way because regional oceanographic process, i.e., fronts (Weingartner 1997) and topographic processes (Blanchard et al. 2013), could affect these fishes' diets and because water depth is an important predictor of sculpin density in the Chukchi (Norcross et al. 2013) and Beaufort Seas (Logerwell et al. 2011). I hypothesized that Arctic Staghorn Sculpin and Shorthorn Sculpin diet compositions would differ from one another in every habitat. Additionally, I investigated resource partitioning between the two species by examining the relationship between their body sizes, mouth gape morphologies, and ultimately the size of prey they consume at similar body sizes. I hypothesized that fish body size was a significant predictor of mouth gape height and width and that body size was a significant predictor of the size of prey each species consumes. Cottidae, i.e., sculpins, is the second most abundant fish family in the Arctic, yet very little is known about their trophic importance. This chapter will add to existing knowledge of these species in the western Arctic and will better inform current and future food web models.

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Chapter 1: A size-based diet comparison of Arctic Cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas[1]

Abstract

Arctic Cod (*Boreogadus saida*) is an important link between upper and lower trophic levels. Previous findings describe differences in its diet throughout the western Arctic, but do not fully explain the causes of this variation. This study compares the stomach contents of Arctic Cod collected over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011) to determine if habitat, i.e., sea of inhabitance, and body size contribute to diet variability. Prey were identified, measured for length, and aggregated into eight major prey categories for analysis. A multivariate method was used to compare the percent mean weight (%MW) of each prey category between seas and fish size classes. Sea of inhabitance, body size, and their interaction accounted for significant variation in Arctic Cod diet composition. Within seas, as body size increased, diets varied both in size and type of prey groups eaten. Between seas, smaller (≤70 mm) fish consumed calanoid copepods, while larger (≥71 mm) fish ate various larger prey. In general, larger Chukchi Sea fish consumed proportionally more benthic prey while Beaufort Sea conspecifics were exclusively pelagic feeders. Documenting habitat and body size specific diet variation could increase our knowledge of Arctic Cod ecology throughout its distribution and enhance current U.S. Arctic food web models.

[1]Gray BP, Norcross BL, Blanchard AL, Beaudreau AH, Seitz AC (in prep.) A size-based diet comparison of Arctic Cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas. Prepared for submission in Polar Biology.

Introduction

Accurately describing the diet compositions of fishes provides the basis for understanding their importance in aquatic food webs (Garvey et al. 1998; Chipps and Garvey 2007). Fish diet composition is influenced by a number of ecological and biological factors, including habitat characteristics and body size (Chipps and Garvey 2007). Aquatic habitat complexity directly influences the amount and type of prey consumed by fishes (Holbrook and Schmitt 1992; Langerhans et al. 2003). Habitat features and complexity may change depending on the physical and biological oceanographic processes unique to that specific habitat (Weingartner 1997; Blanchard et al. 2013; Weingartner et al. 2013). Because fishes are efficient samplers of the prey available in their immediate environments (Hinz et al. 2006), quantifying their diets over large spatial scales could elucidate differences in feeding related to environmental and biological complexity, including habitat and fish body size. Doing so would increase our understanding of Arctic fish ecology, and offer a better parameterization of ecosystem and bioenergetics models (Christensen 1995). The present research focuses on factors that could potentially explain differences in Arctic Cod (*Boreogadus saida*) diets in the northeastern Chukchi and western Beaufort Seas, including shifts in body size and sea of inhabitance.

Arctic Cod is a dominant consumer of zooplankton in the Arctic (Welch et al. 1992; Walkusz et al. 2011). It is one of the most abundant forage fishes throughout its distribution (Lowry and Frost 1981; Bradstreet et al. 1986; Welch et al. 1992; Mecklenburg et al. 2011), and has consistently dominated catches in previous trawl surveys in the western Arctic (Barber et al. 1997; Norcross et al. 2013). It is an important prey species for marine mammals, seabirds, and other fishes (Lowry and Frost 1981, Welch et al. 1992, Walkusz et al. 2011), linking lower

trophic levels to higher level predators (Welch et al. 1992). Arctic Cod is primarily regarded as cryopelagic, i.e., ice-associated (Lønne and Gulliksen 1989), but is found throughout the water column in ice-free areas (Walkusz et al. 2011; Norcross et al. 2013). It is typically a pelagic predator (Lowry and Frost 1981; Lacho 1986), however, Arctic Cod may feed on demersal prey (Cui et al. 2012), especially in shallow shelf areas (Bluhm and Gradinger 2008). Although past research has documented the ecological importance of this species, further study is needed to document its role in Arctic food webs (Walkusz et al. 2011), including those of the northeastern Chukchi Sea (hereafter, Chukchi Sea) and western Beaufort Sea (hereafter, Beaufort Sea).

Arctic Cod diet composition is expected to differ within the Chukchi and Beaufort Seas by fish body size, and between both seas by large-scale differences in biological productivity, prey compositions, and physical oceanography. Within both seas, ontogenetic shifts in diet and gape size likely influence the size range of prey eaten by Arctic Cod (Werner and Gilliam 1984; Rand et al. 2013). Generally, larval Arctic Cod consume smaller stages of calanoid copepods (Bradstreet et al. 1986), while juvenile and adult Arctic Cod consume larger prey, including calanoid copepods, amphipods, mysids, and other fishes (Lowry and Frost 1981; Craig et al. 1982; Jensen et al. 1991). Between both seas, when body size is accounted for; oceanography is expected to explain variability in Arctic Cod diet. Regions of the highly productive and shallow Chukchi Sea shelf (Weingartner 1997; Weingartner et al. 2013) are characterized by favorable, current-driven carbon deposition that supports a predominantly benthic food web (Grebmeier et al. 2006; Blanchard et al. 2013). In contrast, the narrower shelf of the Beaufort Sea receives less nutrient-rich subsidies, and is characterized as less locally productive in terms of both primary (Belkin et al. 2009) and secondary benthic productivity (Carey 1991). These broad-scale differences should be reflected in diet compositions, with Arctic Cod in the Chukchi Sea

possibly consuming proportionally more benthic prey and less pelagic prey than Beaufort Sea conspecifics.

The different habitat characteristics of either sea likely affect the presence and quality of prey consumed by Arctic Cod. Differences in energy content of prey eaten could lead to within-species phenotypic variability (Holbrook and Schmitt 1992). Throughout the western Arctic, published accounts of Arctic Cod diet reveal differences in the prey types consumed by local populations. For example, relative to other western Arctic regions, Arctic Cod in the eastern Bering Sea consume higher proportions of benthic amphipods along with pelagic calanoid copepods (Cui et al. 2012), while conspecifics in the Chukchi (Coyle et al. 1997) and Beaufort Seas (Lowry and Frost 1981; Craig et al. 1982) consume some benthic, but mostly pelagic prey. The differences in major prey types, whether benthic or pelagic in nature, could affect the quality of prey consumed by Arctic Cod. Currently, there are no published studies that address Arctic Cod prey quality. While this study does not directly measure prey energy content, it compares published energy density values for representative prey taxa eaten by Arctic Cod in the Chukchi and Beaufort Seas to determine potential differences in prey quality between seas.

While diet characterizations exist for Arctic Cod in the Chukchi and Beaufort Seas, there is a lack of region-specific, quantitative diet data available for use in food web models (Whitehouse 2013), which furthers the gap in our ecological knowledge of this species. Because of these data limitations, Arctic Cod in the Chukchi Sea food web has recently been modeled using Bering Sea conspecific diet information (Whitehouse 2013). Arctic Cod diet composition can be highly variable depending on local conditions (Walkusz et al. 2011) and body size (Bohn and McElroy 1976; Lowry and Frost 1981). Therefore, using diet composition data from Bering Sea regions as a proxy in the Chukchi Sea could have underestimated or overestimated this

species' effect on pelagic and benthic prey populations. By determining Arctic Cod diet composition in the Chukchi and Beaufort Seas, the appropriateness of applying Bering Sea diet information to the Arctic could be determined.

Most Arctic Cod diet studies throughout the Arctic are small in sample size, from isolated regions, and do not quantitatively account for diet differences due to habitat or fish size. For the present research, Arctic Cod diets were compared within and between the Chukchi and Beaufort Seas (Fig. 1.1). The objectives of this research were 1) to determine whether Arctic Cod diet changes throughout ontogeny within both seas, and 2) to determine if Arctic Cod diet differs between the Chukchi and Beaufort Seas when accounting for size-based variation. These objectives are accomplished through statistical analyses of Arctic Cod diet composition. This information adds to our current knowledge of Arctic Cod ecology by documenting intraspecific diet variability across a large spatial scale, the results of which could better inform food web models in the Chukchi and Beaufort Seas.

Materials and Methods

Sampling areas and methods

Sampling occurred during the ice free months of August and September in both the Chukchi and Beaufort Seas (Fig. 1.1). In the Chukchi Sea, Arctic Cod were collected during three cruises, two that were part of the Alaska Monitoring and Assessment Program (AKMAP; 23 August–03 September, 2010 and 05 September–16 September, 2011), and one cruise that was a part of the Arctic Ecosystem Integrated Survey (Arctic EIS; 13 August–20 September, 2012). These cruises covered the area between Point Hope and the western side of Point Barrow (Fig. 1.1). The AKMAP 2010 cruise transects were south of 70°N latitude (68.43°−69.96°N) and between 167.82°−163.80°W, whereas the AKMAP 2011 cruise occurred north of 70°N

(70.05°−71.30°N) and between 163.75°−157.20°W (Fig. 1.1). Both AKMAP cruises were relatively nearshore surveys (17−60 m depth). The Arctic EIS cruise surveyed about the same extent as both AKMAP cruises (68.50°−73.00°N, 168.50°−157.18°W; Fig. 1.1) and included both nearshore and offshore stations (20−90 m depth). Arctic Cod were collected 17 August−03 September, 2011, in the Beaufort Sea during the Beaufish 2011 survey from the eastern side of Point Barrow to Camden Bay (70.2°−72.2°N, 155.23°−145.07°W; Fig. 1.1). Arctic Cod were collected both inshore and offshore at depths of 13−223 m.

Arctic Cod were caught by towing either a standard plumb staff beam trawl or an otter trawl. Captured fishes were given a lethal dose of MS-222 (i.e., 250 mg/l) mixed with seawater (University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol number 134765; Appendix A). Euthanized fishes were identified using dichotomous keys (Mecklenburg et al. 2002), and after a positive identification, Arctic Cod were frozen in seawater and transported to the UAF Fisheries Oceanography Laboratory for further analyses.

Laboratory methods

All measurements and processes associated with stomach contents analysis took place in the laboratory. Arctic Cod were thawed, individually blotted with tissue paper, weighed to the nearest 0.01 g, and measured for total length in millimeters. Whole stomachs (esophagus to pyloric valve) were removed, placed in petri dishes, and frozen in fresh water until examined. Stomachs were opened and prey was identified using a dissecting microscope. At 6x to 100x magnification, all recognizable prey were identified to the lowest taxonomic level possible, depending on the condition of the stomach contents, with the help of taxonomic keys or personal communication with invertebrate specialists. Once identified, the wet weight value of each prey item was recorded to the nearest 0.0001 g.

Due to the diversity of prey consumed by Arctic Cod, all identifiable prey was aggregated into eight groups based on common taxonomic characteristics for statistical comparisons. These eight groups included benthic amphipods, calanoid copepods, crabs, cumaceans, euphausiids, fish prey, hyperiid amphipods, and "other prey" (Table 1.1). Benthic prey included benthic amphipods and cumaceans, while pelagic prey included calanoid copepods, euphausiids, and hyperiid amphipods. Crabs were either benthic or pelagic depending on life stage, i.e., juveniles and adult crabs were benthic and larval crabs pelagic. Fish prey and "other prey" were either benthic or pelagic depending on the type consumed. "Other prey" included prey that either weighed a very small amount (e.g., barnacle cyprids or harpacticoid copepods, both weighing <0.0001 g) or were rare (e.g., mollusks, mysids, polychaetes, or shrimps). Unidentifiable tissues were removed from analyses because these may have been a variety of soft-bodied prey items, or stomach lining rather than prey.

Data analysis methods

To characterize Arctic Cod diets in the Chukchi and Beaufort Seas, I chose two diet indices, specifically percent mean weight (%MW) and percent occurrence (%O). Percent mean weight was calculated as follows:

$$(1.1) \quad \%MW_i = \frac{1}{P}\sum^{j}\left[\frac{W_{ij}}{\Sigma W_{ij}}\right] \times 100$$

where $\%MW_i$ is the percent mean weight of prey i consumed by a predator, W_{ij} is the weight of prey i in a single predator j, and ΣW_{ij} is the sum of all prey weights in the stomach of a single predator j. The sums of this calculation for each prey item over the entire sample are then divided by the number of fish with food in their stomachs (P). The resulting %MW information can be used as an indicator of the energetic importance of prey types to a fish population (Hyslop 1980; Chipps and Garvey 2007). This index is subjective, however, and has been criticized because one

predator out of population of 100 might eat one heavy prey item yielding a high %MW for that prey for the fish population. In this case, %MW would not accurately document the true importance of this prey. Although there is controversy with %MW (Baker et al. 2014), this index was used in statistical comparisons because %MW is most useful in indicating prey energetic importance (Chipps and Garvey 2007).To accompany %MW, percent occurrence (%O) was calculated because it is a robust and interpretable approach (Baker et al. 2014). This method simply shows the percentage of individuals in the sampled population that ate a specific prey type (Hyslop 1980; Baker et al. 2014). I calculated percent occurrence using the formula:

$$(1.2) \quad \%O = \left[\frac{O_i}{\Sigma P}\right] \text{x } 100$$

where %O is defined as the occurrence of a prey group i divided by the sum of non-empty stomachs (ΣP).

Ontogenetic shifts in Arctic Cod diet were investigated by dividing fish into four size classes: i.e., ≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm. These size classes were developed by analyzing Arctic Cod diet over both seas and determining at what body sizes fish included novel or larger prey types. The smallest size class was Arctic Cod at lengths ≤50 mm because, in general, these fish consumed only calanoid copepods. The 51–70 mm size class represented the first instance of larger prey being included in Arctic Cod diet, such as hyperiid amphipods, crabs, cumaceans, and euphausiids. The 71–100 mm size class represented the first instance of piscivory by Arctic Cod, while the ≥101 mm size class accounted for diet differences for the largest fish. I used these classes in comparisons both within seas among adjacent size classes, and between seas at similar size classes.

To investigate the distribution of prey sizes in Arctic Cod diet, all intact prey items were measured to the nearest 5 mm and divided into three size classes. These prey size classes were as

follows: small (<5 mm), medium (5–10 mm), and large (>10 mm). The percent by number, of small, medium, and large prey sizes in Arctic Cod diets were then plotted against the corresponding fish size classes to identify any patterns in prey consumption.

The sample sizes needed for diet analysis were determined using cumulative prey curves, which plot the occurrence of novel prey against a running total of examined stomachs (Chipps and Garvey 2007). When the curve was close to or at an asymptote, fish diet diversity was said to be adequately described (Chipps and Garvey 2007). Cumulative prey curves (Fig. 1.A-1), indicated that a sample size of about 50 fish stomachs was needed to adequately describe Arctic Cod diet diversity. This sample size was met for all sea and size class groups (Table 1.1), except for ≤50 mm fish in the Chukchi Sea (n=21), consequently this sea and size class group may have been under-represented.

Multivariate techniques were used to simultaneously evaluate differences in prey proportions (Chipps and Garvey 2007) in Arctic Cod diet between seas and size classes. The assumptions of parametric multivariate analysis of variance (MANOVA) were strict, and oftentimes not met when using diet composition data (Chipps and Garvey 2007). Proportional diet data sets contained a multitude of zeroes, which made it difficult to meet distributional assumptions (Quinn and Keough 2002). Because of these issues, I used a permutation-based version of MANOVA based on a Bray-Curtis distance matrix using the function *adonis* (i.e., non-parametric MANOVA, hereafter NP MANOVA) in the vegan package of R, version 2.15.2. This method is considered to be a robust alternative to parametric MANOVA and parametric ordination methods (Legendre and Anderson 1999). The output of this method is a pseudo-*F* statistic analogous to that of MANOVA. If there was a significant difference found between seas and size classes, the same NP MANOVA method was used for multiple comparisons. To account

for the increased likelihood of type 1 error of multiple comparisons, the significance of each multiple comparison was determined using the Holm's sequential Bonferroni-adjusted α value method (Holm 1979).

If the multivariate multiple comparisons indicated significant differences in diet composition between seas and size classes, univariate models (one-way analysis of variance; ANOVA), were used to determine which of the eight prey categories explained those differences. If the ANOVA found significant differences in specific prey categories, Tukey's method of multiple comparisons was used to determine whether differences within and between seas and size classes were significant. Because ontogenetic shifts were of interest, only key comparisons, i.e. adjacent size classes, from the Tukey matrix were presented here. All univariate statistical tests were conducted in R commander version 1.9–6.

Results

The size distribution (Fig. 1.2) and composition of prey (Table 1.1) in the stomachs of 602 Arctic Cod (Chukchi Sea=267 and Beaufort Sea=335) varied between seas and size classes. In both seas, as Arctic Cod body size increased, differences in diets were driven by a general decline in smaller prey eaten, followed by a subsequent increase in larger prey eaten (Fig. 1.2). Of all prey sizes, however, small prey composed the highest proportion of Arctic Cod diet in both seas regardless of size class. NP MANOVA demonstrated a significant interaction in Arctic Cod diet composition between seas and size classes, with diet composition differing between size classes within seas, and between seas within similar size classes (Table 1.2). For Arctic Cod diet in the Chukchi Sea, there was no difference in diet composition between ≤50 mm and 51−70 mm fish (Table 1.3; Fig. 1.3). However, there were significant differences in diet composition between size classes 51−70 mm and 71−100 mm and between 71–100 mm and ≥101 mm. Arctic

Cod diet composition in the Beaufort Sea was significantly different between size classes ≤50 mm and 51−70 mm and between 71–100 mm and ≥101 mm, but not between 51−70 mm and 71−100 mm (Table 1.3; Fig. 1.4). Between the Chukchi and Beaufort Seas, there were no significant differences in small (≤70 mm) Arctic Cod diet composition, but there were significant differences in diets among size classes ≥71 mm (Table 1.3).

Univariate tests highlighted the specific prey types that explained the differences within and between seas by size classes. Combining all Arctic Cod size classes, the ANOVA indicated prey proportions were significantly different for seven of the eight categories (Table 1.4). Although the ANOVA indicated significant differences in euphausiid proportions (Table 1.4), Tukey multiple comparisons did not show significant differences in proportions within or between the Chukchi and Beaufort Seas by size classes. Tukey multiple comparisons revealed that diet differences in the Chukchi Sea between 51−70 mm and 71−100 mm fish size classes were attributed to significantly higher benthic amphipod proportions in 71–100 mm fish and significantly higher calanoid copepod proportions in 51−70 mm fish (Table 1.5). Additionally, in the Chukchi Sea, fish diets in size classes 71–100 mm and ≥101 mm were significantly different mostly due to higher proportions of calanoid copepods in the diets of 71–100 mm fish (Table 1.5). Within the Beaufort Sea, diets of fish in size classes ≤50 mm and 51−70 mm differed due to higher proportions of calanoid copepods in ≤50 mm fish, while diets of fish 51–70 mm and 71–100 mm differed because of higher hyperiid amphipod consumption by 71–100 mm fish (Table 1.5). Comparisons between 71−100 mm and ≥101 mm fish indicated that 71−100 mm fish consumed more calanoid copepods while fish ≥101 mm ate higher proportions of fish prey and hyperiid amphipods (Table 1.5).

Between the Chukchi and Beaufort Seas, Arctic Cod diet composition was not statistically different between the two smaller (≤70 mm) size classes, but was between the two larger size classes (≥71 mm; Table 1.5). Between the two 71−100 mm size classes, there were significantly higher proportions of some benthic prey, including benthic amphipods, cumaceans, and other prey in Chukchi Sea fish diet, and higher proportions of pelagic prey, including calanoid copepods and hyperiid amphipods in Beaufort Sea fish diet, with no difference in proportion of fish prey (Table 1.5). The largest size class fish (≥101 mm) in the Chukchi Sea also consumed significantly higher proportions of benthic amphipods and other prey, while Beaufort Sea conspecifics consumed higher amounts of hyperiid amphipods but each had similar proportions of calanoid copepods, cumaceans, and fish prey (Table 1.5).

Discussion

There is variability in Arctic Cod diet both within and between the Chukchi and Beaufort Seas. In this study, prey were aggregated based on taxonomic likeness and position in the water column. Considering the selected prey groups, Arctic Cod within both seas demonstrated noticeable ontogenetic shifts in both type and proportion of prey consumed, while fish compared between both seas indicated some differences in the major prey types each consumed. Arctic Cod are generalist zooplanktivores (Renaud et al. 2012) whose diets may differ by body size (Lowry and Frost 1981), and food availability within different habitats (Lønne and Gulliksen 1989). This study explains within-sea Arctic Cod diet variability by differences in body sizes, while between-sea variability is likely driven by the effects of large-scale differences in physical and biological oceanography on habitat.

Within the Chukchi and Beaufort Seas, as fish increased in body size, their diet became increasingly varied in both prey taxa and prey size. Increased variability in diet associated with

larger predator body sizes is common among fishes (Labropoulou and Eleftheriou 1997). As fish grow larger, they become more proficient at handling larger, more profitable prey (Werner and Hall 1974); this has been documented in Arctic Cod populations. Smaller cod consume calanoid copepods, while larger individuals integrate larger prey into their diets such as benthic amphipods, euphausiids, fishes, mysids, and shrimps in the Bering (Lowry and Frost 1981; Cui et al. 2012), Chukchi (Lowry and Frost 1981) and Beaufort Seas (Lowry and Frost 1981; Craig et al. 1982). I observed a similar pattern with the smallest fish consuming mostly calanoid copepods and larger individuals consuming larger benthic and pelagic crustaceans and fishes, depending on sea inhabitance. The four size classes (i.e., ≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm) considered in this study highlighted shifts towards the inclusion of novel or larger prey with an increase in fish body size; these selected classes did not isolate the exact body size measurements in which Arctic Cod consumed these specific prey items. Even so, this research suggests Arctic Cod may undergo multiple ontogenetic shifts in diet in the Chukchi and Beaufort Seas. Further, these shifts may occur at similar body sizes in both seas because same-sized Arctic Cod consume very similar sized prey, regardless of prey taxa available in either sea. These patterns could be similar throughout this species' distribution, and if so, accounting for body size would allow a better understanding of Arctic Cod diet throughout multiple ontogenetic stages.

The diet of smaller Arctic Cod (≤70 mm) was similar between the Chukchi and Beaufort Seas and consisted mainly of small (<5 mm) pelagic, calanoid copepods. This similarity may be due to the similar vertical distribution of larval and juvenile Arctic Cod throughout various Arctic regions (Quast 1974; Parker-Stetter et al. 2011; Walkusz et al. 2011), and the prey-handling constraints smaller fish must face (Werner and Gilliam 1984; Woodward and Hildrew 2002). High densities of juvenile Arctic Cod (i.e., ≤40 mm) have been found both in surface

waters and in the water column in the eastern Chukchi Sea (Quast 1974), the U.S. Beaufort Sea (Parker-Stetter et al. 2011), and the Canadian Beaufort Sea (Walkusz et al. 2011). Within surface waters, juvenile Arctic Cod are found to exclusively consume pelagic zooplankton (Walkusz et al. 2011). Small calanoid copepods are documented as the most numerically and likely energetically important prey eaten by juvenile Arctic Cod throughout the Arctic (Lowry and Frost 1981; Bradstreet et al. 1986; Lønne and Gulliksen 1989). The present study supports previous findings by documenting the ecological importance of this prey type to smaller Arctic Cod and indicates that smaller Arctic Cod feeding habits could be similar throughout their distribution.

Larger Arctic Cod (≥71 mm) also primarily consumed pelagic zooplankton in the Chukchi and Beaufort Seas; however, benthic prey was proportionally higher in the diet of Chukchi Sea fish compared to Beaufort Sea conspecifics, a finding that may be related to the differences between the two seas. Arctic Cod mainly feed in the water column (Lønne and Gulliksen 1989), which explains its pelagic diet; however, over shallower Arctic continental shelves, such as the Chukchi Sea, its diet may also be bottom-associated (Bluhm and Gradinger 2008). Relative to Beaufort Sea fish, the two larger size classes of Arctic Cod in the Chukchi Sea consumed higher proportions of benthic amphipods and "other" benthic prey such as polychaetes, bivalves, and mysids. Holding body size constant, this is probably related to the key oceanographic processes that structure Chukchi and Beaufort Sea benthic communities. Regions of the Chukchi Sea are supplemented with warmer water, nutrients (Weingartner 1997), and fauna from the Bering Sea (Walsh et al. 1989). These flow across the Chukchi Sea shelf into the Arctic Ocean, effectively bypassing benthic habitats of the Beaufort Sea, which are instead largely influenced by Arctic and Atlantic waters from the eastern Beaufort Sea (Carey 1991). In

the Chukchi Sea, nutrient-rich subsidies (Walsh et al. 1989), along with high local productivity (Grebmeier et al 2006), are deposited to the benthos, the results of which create positive growth conditions for macrofauna (Feder et al. 1994; Blanchard et al. 2013; Blanchard and Feder 2014). In contrast, the Beaufort Sea receives fewer nutrient subsidies (Belkin et al. 2009) and only about 1–10% of locally generated primary productivity is estimated to reach the benthos (Carey and Ruff 1977; Carey 1987). Consequently, macrofaunal biomass and diversity is lower in regions of the western Beaufort Sea (Carey 1991). Because benthic amphipods and other benthic macrofauna are abundant in areas of the northeastern Chukchi Sea (Blanchard and Feder 2014), the regional processes explained here likely influenced the diet of larger Arctic Cod, making region of inhabitance an important factor in explaining Arctic Cod diet composition.

Combining the present study with published accounts of prey energetics suggests that prey quality for Arctic Cod could change throughout ontogeny and habitats. A diet composed of higher quality prey can improve the body condition and increase survival of fishes (Pinchuk et al. 2013). In the Chukchi and Beaufort Seas, Arctic Cod ≤70 mm in length mainly feed on calanoid copepods, two of the most common species being *Calanus hyperboreus* and *C. glacialis*. Respectively, each is 64% and 56% lipid by dry mass (Lee 1975). Both species are relatively small (≤8 mm), but very lipid rich, which might explain why larger Arctic Cod in both seas continue to consume them. Other than calanoid copepods, larger Arctic Cod consumed larger pelagic zooplankton, such as hyperiid amphipods. This prey was consumed by fish ≥71 mm in both seas, but mostly by those in the Beaufort Sea. In contrast, Chukchi Sea conspecifics consumed higher proportions of benthic amphipods. Therefore, it is possible that Arctic Cod, by consuming disproportionate amounts of pelagic or benthic prey, could experience prey quality differences between the Chukchi and Beaufort Seas. In this study, the two most abundant benthic

amphipod families consumed by Arctic Cod in the Chukchi Sea were Ampeliscidae and Oedicerotidae. Energetic values of representative species of these families (*Ampelisca eschrichtii*, Ampeliscidae; and *Pareodiceros lynceus*, Oedicerotidae) were about 10.5% and 7.1% lipid by dry mass near Svalbard (Legezynska et al. 2012). *Themisto libellula* was the most common hyperiid amphipod consumed by Arctic Cod in the Beaufort Sea and had a lipid content of 18–35% of dry mass in the Labrador Sea (Percy and Fife 1981). If lipid values are similar among amphipods throughout their global distribution, then Arctic Cod in the Beaufort Sea would be consuming a more lipid-rich diet, due to greater proportions of pelagic prey. However, the energy content of prey can vary spatially and temporally due to environmental variability (Percy and Fife 1981; Hartman and Brant 1995). To account for this variability, it would be necessary to relate Arctic Cod distribution patterns to regional diet quality and determine if differences in Arctic Cod body condition exist. This type of study could give insight into their ecology at the population level.

The between-sea differences in Arctic Cod diet composition documented in this study have implications for food web modeling. Historically, there has been a lack of quantitative, region-specific diet data for Arctic Cod in the Chukchi Sea. As a result, food web models for this area have relied on conspecific diet data collected in the eastern Bering Sea (Whitehouse 2013). A recent model parameterized Arctic Cod diet composition as follows: 23% benthic amphipods, 17% copepods, 48% other zooplankton, 6% miscellaneous crustaceans, 2% shrimps, with the remaining 2% made up of fishes, bivalves, miscellaneous crabs, and polychaetes (Whitehouse 2013). Comparing the model diet composition with our results indicates that applying these model parameters would underestimate the importance of calanoid copepods in both seas, and overestimate the amount of benthic amphipods eaten in the Beaufort Sea. Arctic Cod diet can

vary depending on local prey availability (Craig et al. 1982; Lønne and Gulliksen 1989; Renaud et al. 2012) and fish body size (Lowry and Frost 1981); thus, the accuracy of food web models would be enhanced by accounting for size-dependent and regional variation in diet.

This study shows that Arctic Cod diet differs both within and between the Chukchi and Beaufort Seas and varies according to body size. Variability within seas was related to ontogenetic shifts in body size and morphology that allowed larger fish to include larger prey in their diets. However, body size was likely not the only source of within-sea diet variability. Smaller-spatial scale processes, such as the effects of regional oceanographic and topological characteristics (Lønne and Gulliksen 1989; Blanchard and Feder 2014) on invertebrate assemblages (Ashjian et al. 2005; Blanchard et al. 2013) also could have attributed to within and between sea variability. Fish $\leq$70 mm in length fed similarly in both seas, whereas larger fish diets were different and probably reflected the regionally available prey community. These findings provide insight into the role of Arctic Cod as a predator in the Arctic, and suggest that the importance of specific prey may vary depending on body size and habitat. Future work could examine diets in relation to available pelagic and benthic invertebrate density data to evaluate the degree to which cod are selective foragers. Further, the population-level effects of prey quality on Arctic Cod in the Chukchi and Beaufort Seas could be investigated by examining variation in fish condition and size related to the lipid content of prey eaten by Arctic Cod. This research, along with future avenues of study, will be useful in describing the ecological role of Arctic Cod in the Chukchi and Beaufort Sea food web.

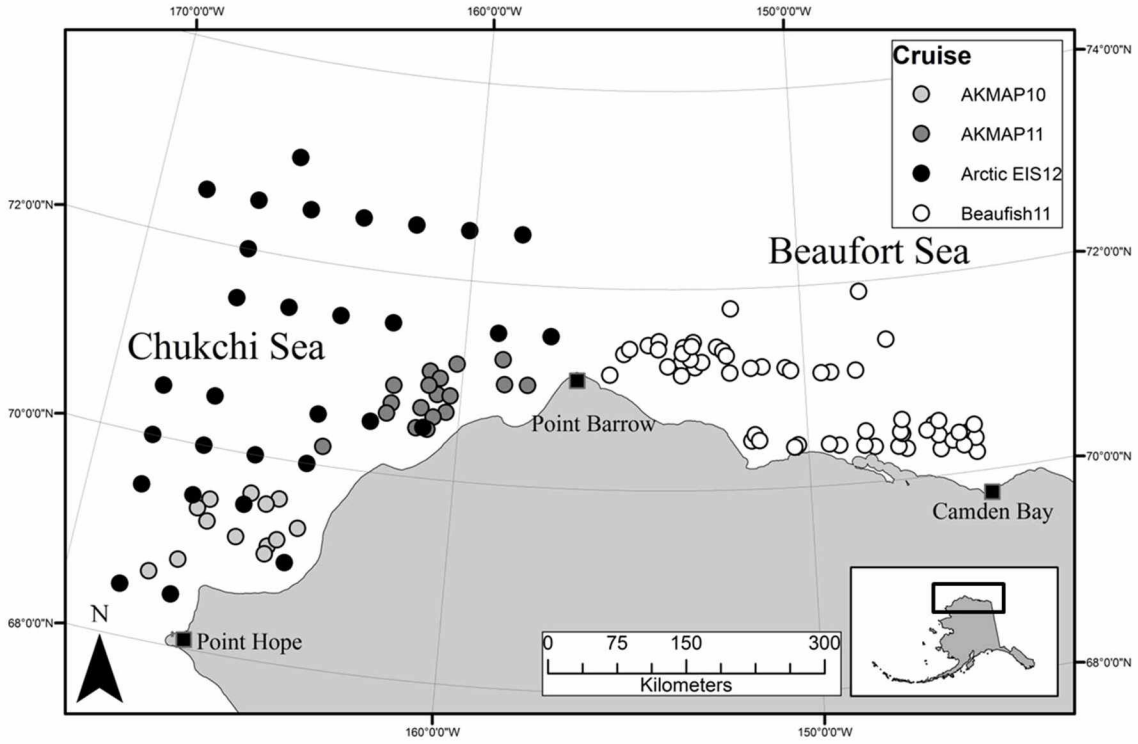

Fig. 1.1 Arctic Cod diet analysis sampling locations in the Chukchi and Beaufort Seas. Fish were collected over four cruises, three in the Chukchi Sea (AKMAP10–11 and ArcticEIS12), and one in the Beaufort Sea (Beaufish11).

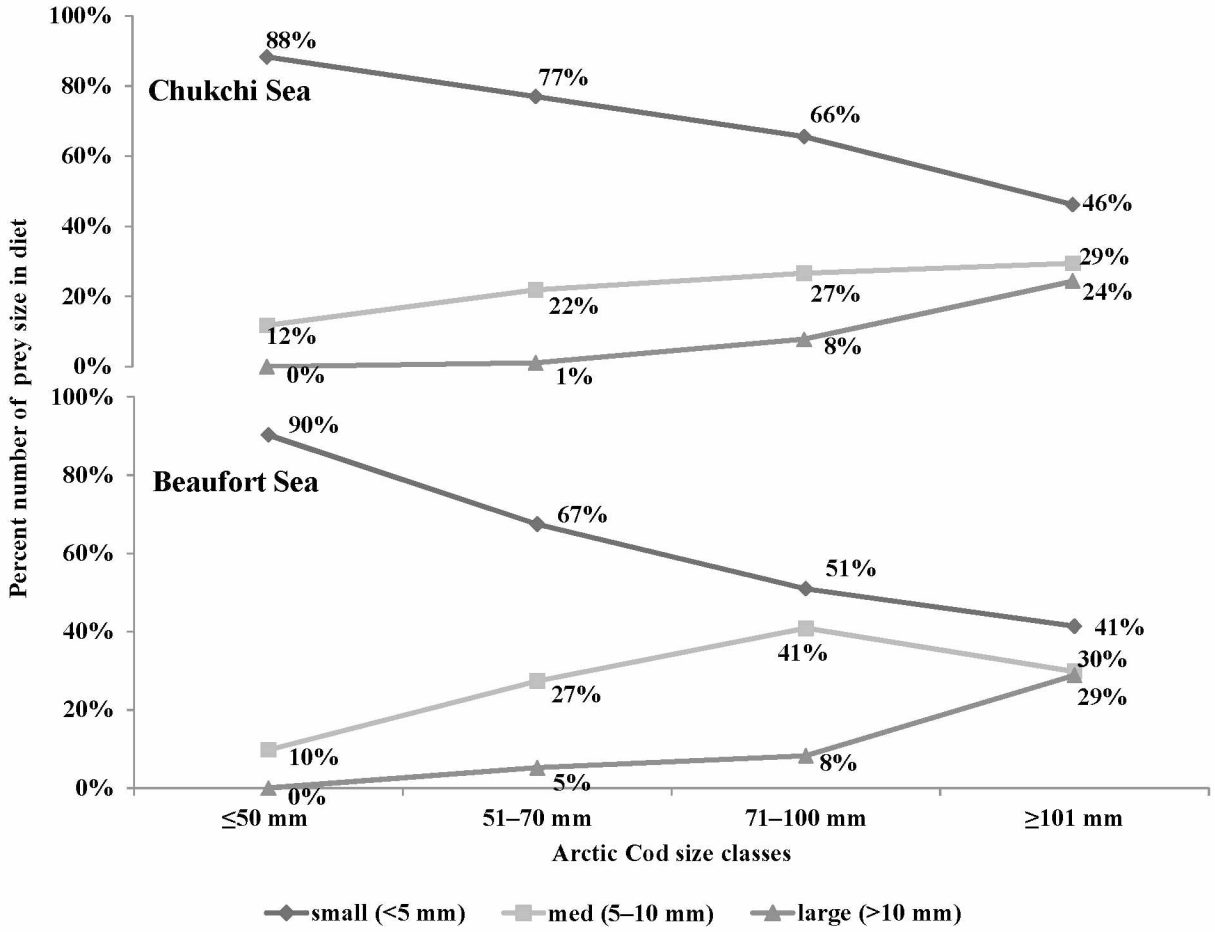

Fig. 1.2 The percent number of small (<5 mm), medium (5–10 mm), and large (>10 mm) prey eaten by four size classes of Arctic Cod (≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm) in the Chukchi and Beaufort Seas.

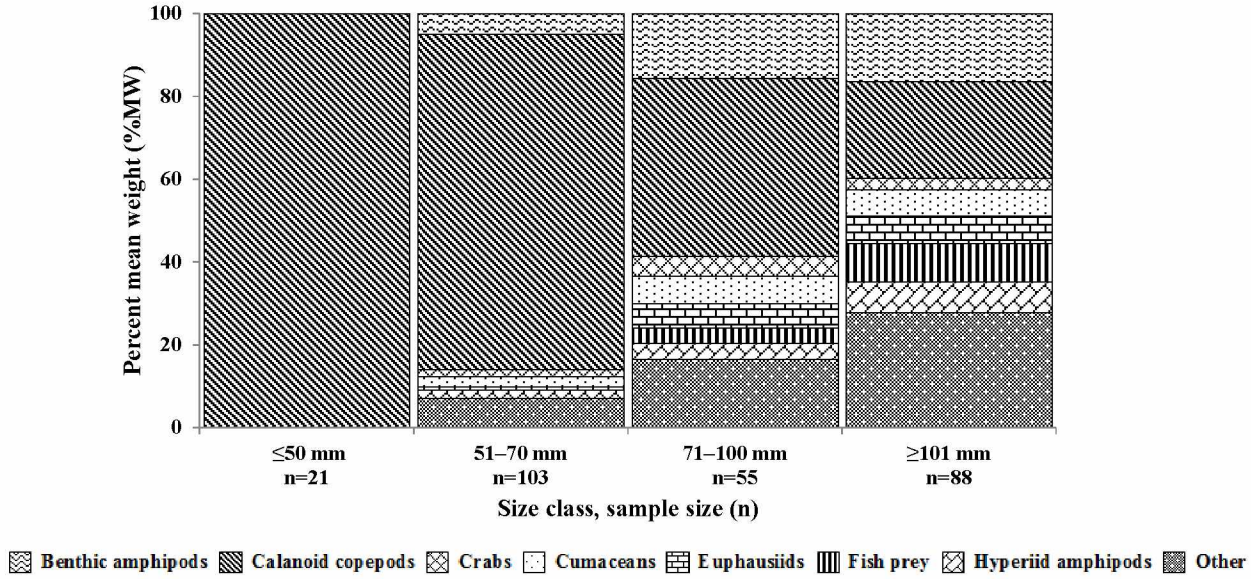

Fig. 1.3 Percent mean weight (%MW) of prey eaten by Arctic Cod in the Chukchi Sea for four size classes (≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm).

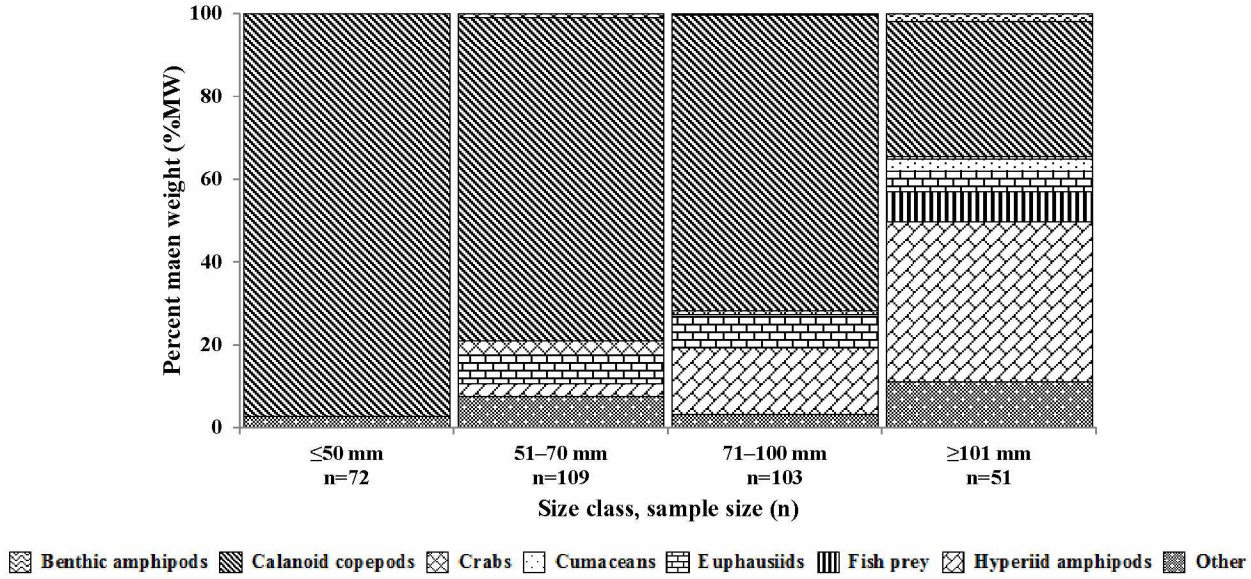

Fig. 1.4 Percent mean weight (%MW) of prey eaten by Arctic Cod in the Beaufort Sea for four size classes (≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm).

Table 1.1 Arctic Cod diet summarized for the Chukchi and Beaufort Seas and all size classes by percent mean weight (%MW) and percent occurrence (%O). Major prey categories used in analyses are in boldface; prey items contributing to the major categories are listed underneath. Total number of prey, total prey weight (g), and total stomachs are listed at the end of the table.

Arctic Cod diet	Chukchi Sea – Size class, %MW (%O)				Beaufort Sea – Size class, %MW (%O)			
Prey Categories	≤50 mm	51–70 mm	71–100 mm	≥101 mm	≤50 mm	51–70 mm	71–100 mm	≥101 mm
Benthic amphipods	-	5.0 (11)	15.7 (31)	16.4 (39)	-	0.9 (1)	0.3 (2)	1.9 (4)
Ampelescidae	-	0.3 (1)	2.7 (4)	2.5 (3)	-	-	-	0.3 (2)
Atylidae	-	0.3 (3)	-	0.1 (2)	-	-	-	-
Oedicerotidae	-	0.1 (1)	1.7 (9)	0.9 (13)	-	-	0.1 (1)	-
Other Benthic amphipods	-	4.3 (9)	11.2 (20)	12.9 (31)	-	0.9 (1)	0.2 (2)	1.6 (2)
Calanoid copepods	100 (100)	80.9 (91)	43.0 (67)	23.3 (44)	97.2 (97)	78.2 (87)	71.4 (84)	32.7 (65)
Calanus glacialis	48.0 (76)	36.1 (78)	22.0 (42)	15.1 (35)	49.6 (68)	36 (67)	8.6 (37)	8.4 (39)
Calanus hyperboreus	4.8 (5)	4.4 (13)	2.3 (4)	0.9 (7)	10.5 (15)	20.6 (36)	42.3 (62)	15.6 (33)
Metridia longa	0.8 (5)	-	0.4 (2)	0.1 (1)	3.7 (10)	2.0 (11)	3.0 (25)	0.1 (10)
Other Calanoid copepods	46.4 (67)	40.5 (71)	18.3 (40)	7.3 (23)	33.4 (54)	19.5 (43)	17.6 (42)	8.5 (29)
Crabs	-	1.7 (3)	4.8 (9)	2.8 (7)	-	3.4 (6)	1.0 (5)	0.5 (8)
Hyas coarctatus	-	-	-	0.9 (1)	-	-	-	-
Paguridae	-	0.6 (1)	1.2 (6)	0.8 (5)	-	2.2 (3)	1.0 (4)	0.2 (4)
Other Crabs	-	1.1 (2)	3.6 (6)	1.1 (1)	-	1.2 (3)	0.1 (1)	0.3 (4)
Cumaceans	-	2.5 (9)	6.7 (24)	6.3 (26)	-	-	0.5 (3)	3.0 (8)
Diastylidae	-	0.5 (1)	0.6 (4)	0.6 (2)	-	-	-	-
Leuconidae	-	0.2 (1)	2.2 (9)	3.1 (14)	-	-	0.5 (2)	3.0 (6)
Nannastacidae	-	0.5 (3)	2.3 (6)	0.4 (5)	-	-	-	-
Other Cumaceans	-	1.2 (6)	1.7 (9)	2.1 (11)	-	-	0.1 (1)	0.1 (2)
Euphausiids	-	0.8 (1)	5.8 (7)	6.7 (17)	-	6.8 (8)	7.6 (13)	4.9 (14)
Thysanoessa raschi	-	0.8 (1)	5.8 (7)	6.7 (17)	-	6.8 (8)	7.6 (13)	4.9 (14)
Fish prey	-	-	3.6 (4)	9.2 (14)	-	0.1 (1)	-	7.4 (18)
Gadidae	-	-	-	1.0 (1)	-	-	-	-
Stichaeidae	-	-	-	1.0 (1)	-	-	-	-
Other Fish prey	-	-	3.6 (4)	7.2 (11)	-	0.1 (1)	-	7.4 (18)
Hyperiid amphipods	-	2.0 (4)	3.9 (7)	7.4 (21)	-	3.2 (7)	16 (31)	38.6 (61)
Themisto abysorrum	-	2.0 (4)	1.3 (6)	0.3 (5)	-	0.1 (2)	2.6 (14)	5.4 (18)
Themisto libellula	-	-	1.6 (2)	5.6 (11)	-	1.8 (2)	7.1 (9)	14 (22)
Themisto spp.	-	-	1.0 (2)	1.5 (5)	-	1.2 (4)	6.3 (16)	19.3 (39)
Other	-	7.0 (17)	16.5 (29)	27.8 (41)	2.8 (2.8)	7.5 (11)	3.2 (12)	11.1 (24)
Mollusks	-	-	-	-	-	-	0.1 (1)	0.1 (2)
Mysids	-	-	-	2.2 (2)	-	3.1 (4)	0.1 (1)	1.5 (6)
Polychaeates	-	-	1.5 (6)	2.4 (7)	-	-	0.1 (1)	-
Shrimps	-	-	0.1 (2)	4.0 (10)	-	-	0.9 (1)	0.3 (2)
All Other	-	7.0 (17)	14.9 (24)	19.1 (32)	2.8 (3)	4.4 (7)	2.3 (10)	9.2 (20)
Total number of prey	263	1666	1508	3670	952	1123	1382	1098
Total prey weight (g)	0.1	1.0	1.7	10.0	0.3	1.8	6.4	7.1
Total stomachs	21	103	55	88	72	109	103	51

Table 1.2 Overall NP MANOVA model results of differences in Arctic Cod diets between the Chukchi and Beaufort Seas and among size classes.

Variable(s)	*df*	*F*	*p*
Sea	1	23.56	<0.001
Size class	3	31.91	<0.001
Sea*Size class	3	5.638	<0.001

Table 1.3 Multiple comparisons using NP MANOVA to determine significant differences in Arctic Cod diet compositions between seas and among size classes. To account for the increased probability of type 1 error related to multiple comparisons, p-values were compared to the Holm's sequential Bonferroni adjusted significance level (i.e., *adj*-α). If the p-value was less than the *adj*-α the null hypothesis (H0:) of no difference in diet compositions was rejected.

Seas vs. Size classes (*df=1)*	*F*	*p*	*adj*-α	Reject H0:
Chukchi Sea (≤50 mm vs. 51−70 mm)	3.123	0.029	0.017	no
Chukchi Sea (51−70 mm vs. 71−100 mm)	15.268	<0.001	0.005	yes
Chukchi Sea (71−100 mm vs. ≥101 mm)	2.974	0.007	0.010	yes
Beaufort Sea (≤50 mm vs. 51−70 mm)	7.945	0.002	0.008	yes
Beaufort Sea (51−70 mm vs. 71−100 mm)	4.134	0.019	0.013	no
Beaufort Sea (71−100 mm vs. ≥101 mm)	15.834	<0.001	0.005	yes
Chukchi Sea vs. Beaufort Sea (≤50 mm)	0.587	1.000	0.050	no
Chukchi Sea vs. Beaufort Sea (51−70 mm)	1.893	0.105	0.025	no
Chukchi Sea vs. Beaufort Sea (71−100 mm)	11.432	<0.001	0.006	yes
Chukchi Sea vs. Beaufort Sea (≥101 mm)	9.054	<0.001	0.007	yes

Table 1.4 Mean percent weight (%MW) of major prey items consumed by Arctic Cod in the Chukchi and Beaufort Seas compared using one-way ANOVA.

Prey categories (*df*=7)	*F*	*p*
Benthic amphipods[B]	10.21	<0.001
Calanoid copepods[P]	40.87	<0.001
Crabs[B/P]	1.254	0.271
Cumaceans[B]	3.869	<0.001
Euphausiids[P]	2.148	0.037
Fish prey[B/P]	5.988	<0.001
Hyperiid amphipods[P]	18.65	<0.001
Other prey[B/P]	9.188	<0.001

[B] Benthic prey
[P] Pelagic prey

Table 1.5 Tukey multiple comparisons of major prey types consumed by four size classes (≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm) of Arctic Cod in the Chukchi and Beaufort Seas. Significant differences in diet compositions are denoted by a boldfaced *t* statistic and *p*-value. The sea or size class in which diet proportions of a certain prey were higher is in parenthesis below the *t* statistic and *p* value. There were no significant differences in euphausiid or crab proportions; therefore they are not reported here.

Seas vs. Size classes (*df*=7)	Benthic amphipods[B]	Calanoid copepods[P]	Cumaceans[B]	Fish prey[B/P]	Hyperiid amphipods[P]	Other prey[B/P]
Chukchi (≤50 vs. 51–70)	t=1.131 p=0.947	t=-2.176 p=0.355	t=0.856 p=0.989	t=0.000 p=1.000	t=0.373 p=0.999	t=1.136 p=0.946
Chukchi (51–70 vs. 71–100)	**t=3.419** **p=0.014** **(71–100)**	**t=-6.216** **p<0.001** **(51–70)**	t=2.106 p=0.400	t=1.603 p=0.739	t=0.498 p=1.000	t=2.218 p=0.331
Chukchi (71–100 vs. ≥101)	t=0.246 p=1.000	**t=-3.128** **p=0.037** **(71–100)**	t=-0.185 p=1.000	t=2.376 p=0.245	t=0.910 p=0.984	t=2.555 p=0.167
Beaufort (≤50 vs. 51–70)	t=0.325 p=0.999	**t=-3.429** **p=0.014** **(≤50)**	t=0.000 p=1.000	t=0.000 p=1.000	t=0.922 p=0.983	t=1.216 p=0.923
Beaufort (51–70 vs. 71–100)	t=-0.254 p=1.000	t=-1.340 p=0.877	t=0.289 p=1.000	t=0.000 p=1.000	**t=4.115** **p<0.001** **(71–100)**	t=1.225 p=0.920
Beaufort (71–100 vs. ≥101)	t=0.502 p=0.999	**t=-6.192** **p<0.001** **(71–100)**	t=1.232 p=0.918	**t=3.167** **p=0.033** **(≥101)**	**t=5.800** **p<0.001** **(≥101)**	t=1.794 p=0.612
Chukchi vs. Beaufort (≤50)	t=0.000 p=1.000	t=-0.306 p=1.000	t=0.000 p=1.000	t=0.000 p=1.000	t=0.000 p=1.000	t=0.436 p=1.000
Chukchi vs. Beaufort (51–70)	t=-1.612 p=0.733	t=-0.551 p=0.999	t=-1.491 p=0.804	t=0.000 p=1.000	t=0.369 p=1.000	t=0.152 p=1.000
Chukchi vs. Beaufort (71–100)	**t=-4.954** **p<0.001** **(Chukchi)**	**t=4.660** **p<0.001** **(Beaufort)**	**t=-3.095** **p=0.040** **(Chukchi)**	t=-1.603 p=0.739	**t=3.200** **p=0.029** **(Beaufort)**	**t=-3.100** **p=0.040** **(Chukchi)**
Chukchi vs. Beaufort (≥101)	**t=-4.453** **p<0.001** **(Chukchi)**	t=1.454 p=0.824	t=-1.558 p=0.766	t=-0.760 p=0.995	**t=7.857** **p<0.001** **(Beaufort)**	**t=-3.693** **p=0.006** **(Chukchi)**

[B] Benthic prey
[P] Pelagic prey

Appendix 1.A

Arctic Cod cumulative prey curves

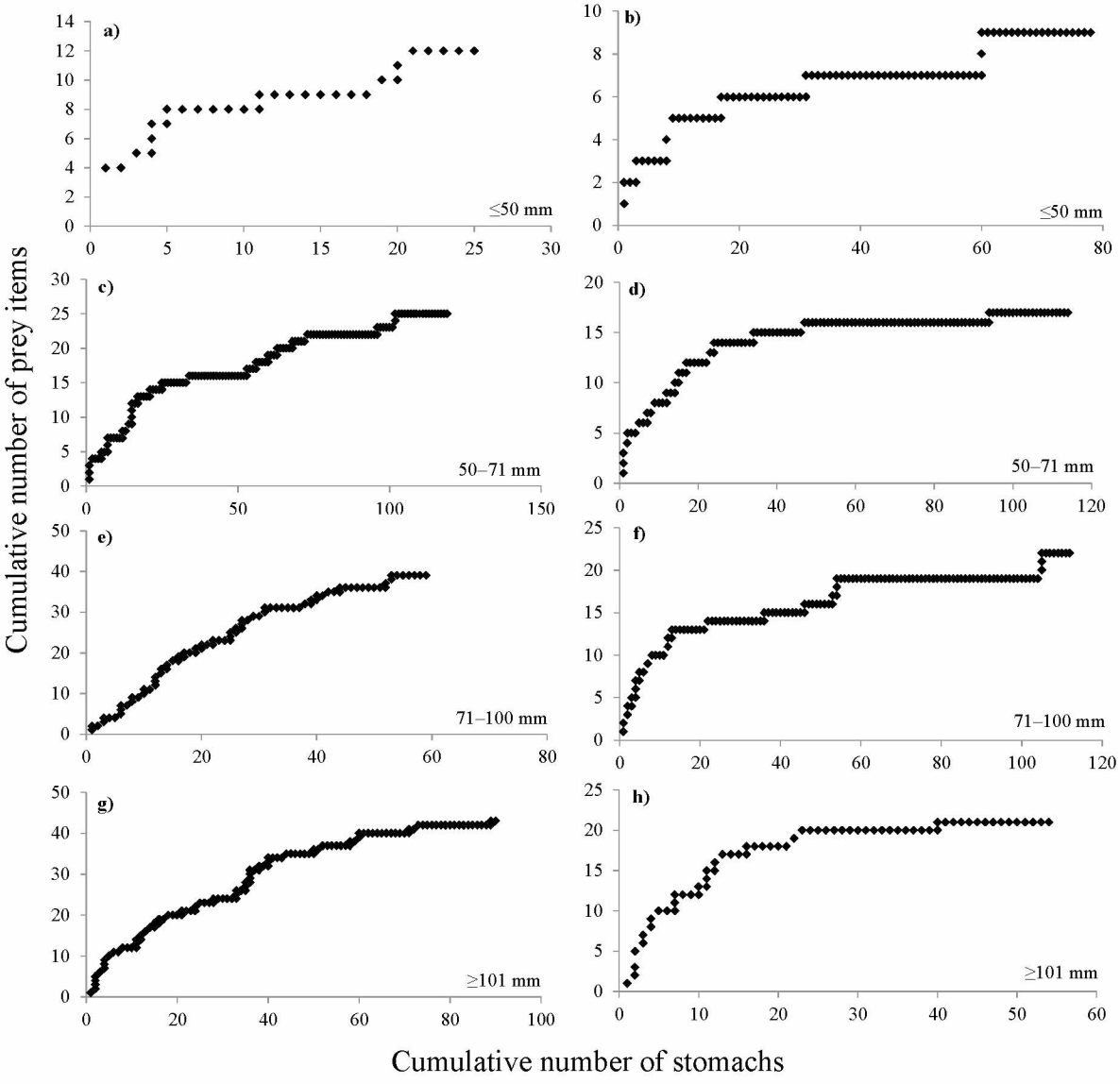

Fig. 1.A-1 Cumulative prey curves indicating the sample size needed to adequately describe Arctic Cod diet. When the curve is at or near its asymptote, the diet is considered adequately described. Letters a, c, e, and g are Chukchi Sea fish, while letters b, d, f, and h are Beaufort Sea fish. Size classes are noted in the bottom right hand corner of each figure.

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Chapter 2: Region, depth, and size-based diet comparisons of two confamilial sculpins: Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*) and Shorthorn Sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort Seas[2]

Abstract

Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*) and Shorthorn Sculpin (*Myoxocephalus scorpius*) belong to Cottidae, the second most abundant fish family in the western Arctic. Although considered important in food webs, little is known about these sculpins' diets and their ecological interactions throughout this area. This research compares the stomach contents of both species collected over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011), and investigates interspecific diet variability due to habitat, body size, and mouth morphology. Prey was identified, measured for length, and aggregated into nine major categories for analysis. A multivariate method was used to compare the percent mean weight (%MW) of each prey category between habitats. Regression techniques were used to investigate differences in mouth morphologies and prey size versus predator size. In general, both species were generalist feeders in all examined habitats. Arctic Staghorn Sculpin fed exclusively on benthic prey while Shorthorn Sculpin consumed both benthic and pelagic prey. Of the two species, Shorthorn Sculpin mouth dimensions were larger; consequently, it consumed larger prey and generally a wider breadth of prey taxa. These findings indicate both sculpins partition available prey resources in shared habitats. This study increases knowledge of sculpin feeding ecology in the western Arctic and offers regional, quantitative diet information that could enhance current U.S. Arctic food web models.

[1]Gray BP, Norcross BL, Blanchard AL, Beaudreau AH, Seitz AC (in prep.) Region, depth, and size-based diet comparisons of two confamilial sculpins: Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*) and Shorthorn Sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort Seas. Prepared for submission in Deep Sea Research Part II: Topical Studies in Oceanography

Introduction

Fishes in the Arctic ecosystem provide an important link between lower and higher trophic level organisms (Lowry and Frost 1981; Bradstreet and Cross 1982; Craig et al. 1982; Atkinson and Percy 1992), yet the feeding ecology of Arctic marine fishes and their roles in food webs are poorly understood (Mecklenburg et al. 2008). These knowledge gaps limit the ability to document energy flows throughout this vast system. Because fishes consume a subset of the prey available in their immediate environments (Hinz et al. 2006), examining their diets over large spatial scales could enhance current efforts in food web modeling and increase understanding of Arctic fish ecology. To address these needs, the present research uses stomach contents analysis to comprehensively describe and compare the diets of two abundant fish species throughout the western Arctic.

Collectively, sculpins (family Cottidae) are commonplace in the western Arctic (Barber et al. 1997; Norcross et al. 2013) and are important in the northeastern Chukchi (hereafter Chukchi Sea) and western Beaufort Seas (hereafter Beaufort Sea) as both prey (Lowry et al. 1980; Smith et al. 1997; Rand et al. 2013) and predators (Moore and Moore 1974; Atkinson and Percy 1992; Coyle et al. 1997). Two abundant species belonging to this family include Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*) and Shorthorn Sculpin (*Myoxocephalus scorpius*; Mecklenburg et al. 2011).These species make ideal candidates for food habits studies given their abundance and documented importance in Arctic food webs. Arctic Staghorn Sculpin is prey for seals (Lowry et al. 1980; Smith et al. 1997) and other fishes (Coyle et al. 1997) while Shorthorn Sculpin is preyed on by Arctic Cod (*Boreogadus saida*; Rand et al. 2013) and likely some marine mammals. As predators, both sculpins are benthic generalists (Moore and Moore 1974; Atkinson and Percy 1992; Coyle et al. 1997; Cui et al. 2012). Arctic Staghorn Sculpin in the eastern

Bering Sea (Cui et al. 2012), Chukchi (Coyle et al. 1997), and southeastern Beaufort Seas (Atkinson and Percy 1992) consume fairly similar diets consisting of benthic amphipods, bivalve siphons, cumaceans, and polychaetes. There is no published diet information for Shorthorn Sculpin in the Chukchi and Beaufort Seas, however, this species consumes mostly crabs and benthic amphipods in the eastern Bering Sea (Cui et al. 2012), benthic crustaceans, decapods, and polychaetes in the Labrador Sea (Moore and Moore 1974; Atkinson and Percy 1992), and benthic crustaceans and fishes in the southwestern Baltic Sea (Cardinale 2000). These previous studies indicate the possibility of similarities between the two species' diets, and that Shorthorn Sculpin diet may be more regionally variable than that of Arctic Staghorn Sculpin.

Habitat features in the Chukchi or Beaufort Seas likely influence the prey available to both sculpins. This study specifically considers the effects of water depth and region of inhabitance on Arctic Staghorn Sculpin and Shorthorn Sculpin diets. Water depth is an important predictor of sculpin density in the Chukchi Sea (Norcross et al. 2013) and Beaufort Sea (Logerwell et al. 2011), but has less influence in structuring macrofaunal communities (i.e., potential prey for sculpins, Blanchard et al. 2013) than carbon availability to the benthos (Grebmeier et al. 1989). The Chukchi Sea is a productive (Grebmeier et al. 2006), shallow system that is supplemented by nutrients (Weingartner 1997; Weingartner et al. 2013) and fauna (Walsh et al. 1989) of Bering Sea origin. The high local production, external nutrient input, and small-scale oceanographic processes drive the strong delivery of carbon to the benthos in the Chukchi Sea (Grebmeier et al. 2006), which creates positive growth conditions for benthic macrofauna (Feder et al. 1994a; Blanchard et al. 2013; Blanchard and Feder 2014). Comparatively, macrofaunal biomass and diversity is lower in regions of the Beaufort Sea (Carey 1991). This is likely because the deeper, narrower western Beaufort Sea shelf receives

fewer nutrient subsidies (Belkin et al. 2009; Crawford et al. 2012) with only about 10% of the locally originated nutrients reaching the benthos (Carey and Ruff 1977; Carey 1987). These broad differences in productivity should be reflected in the sculpins' diets, with more diversity in prey taxa observed for both species in the Chukchi Sea.

Arctic Staghorn Sculpin and Shorthorn Sculpin differ in body morphology, which should influence each species' pattern of prey consumption. Shorthorn Sculpin can achieve larger sizes than Arctic Staghorn Sculpin (Mecklenburg et al. 2002) and body size influences foraging success (Scharf et al. 2000). As fishes attain greater body sizes, mouth morphology characteristics, i.e., gape width and height, increase (Scharf et al. 2000) and greatly influence the maximum size of prey eaten by fishes (Keast and Webb 1966; Werner and Gilliam 1984; Juanes et al. 2002). Typically, the size range of prey consumed by larger fishes overlaps that of smaller ones and could give larger fishes a competitive advantage (Scharf et al. 2000). However, morphological differences could affect food resource partitioning (Ross 1986), allowing sculpins to share habitats.

Despite previous diet characterizations in the western Arctic, there is a lack of quantitative, region-specific diet information available for Arctic Staghorn Sculpin and Shorthorn Sculpin (Whitehouse 2013), which could have implications for food web models. Recently, Whitehouse (2013) included Arctic Staghorn Sculpin and Shorthorn Sculpin in two separate functional groups, i.e., "other sculpins" and "large-mouth sculpin," respectively, in a food web model constructed for the eastern Chukchi Sea (Whitehouse 2013). The diet compositions of these functional groups were parameterized using diet information from eastern Bering Sea studies. Because fishes' diets can be quite variable throughout ontogeny and habitat (Chipps and Garvey 2007) using spatially-distant, confamilial diet information as a proxy for the

sculpin's diets in food web models could misrepresent their ecological impact in the western Arctic. Characterizing and comparing these species' diets throughout the Chukchi and Beaufort Seas could determine the appropriateness of borrowing sculpin diet data from other regions to parameterize food web models.

The objectives of this research are to 1) produce a comprehensive characterization of two confamilial sculpin species' diets in the Chukchi and Beaufort Seas and quantify variation in diet related to habitat, i.e., sea-region and depth, 2) statistically compare Arctic Staghorn Sculpin and Shorthorn Sculpin diets to determine significant differences in prey use, 3) analyze the morphological differences between the two sculpin species, and 4) relate those morphological differences to variability in sizes of prey consumed. Arctic Staghorn Sculpin and Shorthorn Sculpin diet compositions are expected to differ throughout all examined habitats. Additionally, differences in body size and mouth morphologies are expected to influence the size of prey consumed by each species. Using stomach contents analysis and other quantitative techniques, this research indicates that within similar habitats in the western Arctic, differences in body size and morphology may enhance resource partitioning between these confamilial sculpins.

Materials and Methods

Sampling areas and methods.

Sampling took place during the ice free months (August-September) in the Chukchi and Beaufort Seas (Fig. 2.1). In the Chukchi Sea, Arctic Staghorn Sculpin and Shorthorn Sculpin were collected over three cruises, two that were a part of the Alaska Monitoring and Assessment Program (AKMAP; 23 August–03 September, 2010 and 05 September–16 September, 2011) and one cruise that was a part of the Arctic Ecosystem Integrated Survey (Arctic EIS;13 August–20 September, 2012). These cruises covered the area between Point Hope and the western side of

Point Barrow (Fig. 2.1). Chukchi Sea regions were divided at 70°N, with the south Chukchi study area (hereafter, SCS) falling below 70°N and the north Chukchi (hereafter, NCS) above 70°N. The AKMAP 2010 cruise transects occurred in the SCS region between latitudes 68.43°−69.96°N and longitudes 167.82°−163.80°W, whereas the AKMAP 2011 cruise occurred in the NCS region between latitudes 70.05°−71.30°N and longitudes 163.75°−157.20°W (Fig.2.1). Both AKMAP cruises were relatively nearshore surveys (17−60 m water depth). The Arctic EIS cruise surveyed about the same latitudinal extent as both AKMAP cruises (Fig. 2.1). Trawling occurred in both the SCS and NCS regions between latitudes 68.50°−73.00°N and longitudes 168.50°−157.18°W, including both nearshore and further offshore stations (20−90 m water depth). Sculpins were collected in the Beaufort Sea during the Beaufish 2011 cruise between the eastern side of Point Barrow and Camden Bay (Fig. 2.1). Sampling took place during 17 August–03 September, above 70°N latitude (70.2°−72.2°N) and between longitudes 155.23°−145.07°W. Transects were divided at 151.75°W into the west Beaufort and east Beaufort regions (hereafter referred to as WBS and EBS, respectively). Fishes were taken both inshore and offshore at depths of 13−223 m.

Region (i.e., SCS, NCS, WBS, or EBS) and depth (i.e., ≤30 m or >30 m) divisions within each region were developed to either highlight regional oceanographic processes that could affect benthic productivity, or to even out sample sizes for statistical analyses. Frontal boundaries were expected to increase benthic productivity by concentrating and exporting pelagic nutrients to the benthos (Feder et al. 1994b). The two frontal boundaries accounted for in this research occur in the shallower waters (≤30 m) of the SCS near Point Hope and in the NCS near Point Franklin (Weingartner 1997; Fig. 2.1). Additionally, in the deeper waters (>30 m) of the NCS, benthic productivity may have been increased by the hydrographic and topographic

features associated with Hanna Shoal (Blanchard et al. 2013) and Barrow Canyon (Blanchard and Feder 2014; Fig. 2.1). There were no other documented fronts or well-known oceanographic features to account for in the other region and depth categories. All other region and depth categories were mainly developed to even sample sizes for statistical analyses, although differences between the sculpin's diets were expected. Comparisons were not made in the EBS at depths >30 m due to very small samples sizes of Shorthorn Sculpin.

Arctic Staghorn Sculpin and Shorthorn Sculpin were captured by towing either a standard plumb staff beam trawl (PSBT) or two types of otter trawls. Nets differed in dimension and tow speed. The PSBT had a 3 m beam, a 4 mm mesh codend, and was towed at 1 to 2 knots for 2 to 5 minutes. The smaller otter trawl had a 9.1 m opening, a 19 mm codend and was towed at 2 to 2.5 knots for 5 to 10 minutes. The larger otter trawl (NOAA 83-112 net) had on average a 15 m opening, a 40 mm codend, and was towed at about 4 knots for 15 minutes. Using all three nets was useful in sampling all life stages of sculpins. Captured fishes were given a lethal dose of MS-222 (i.e., 250 mg/l) mixed with seawater (University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol number 134765; Appendix A). Euthanized fishes were identified using dichotomous keys (Mecklenburg et al. 2002) and after a positive identification, Arctic Staghorn Sculpin and Shorthorn Sculpin were frozen in seawater and transported to the UAF Fisheries Oceanography Laboratory for further analyses.

Laboratory methods

All measurements and processing associated with stomach contents analysis took place in the laboratory. Arctic Staghorn Sculpin and Shorthorn Sculpin were thawed, individually blotted with tissue paper, weighed to the nearest 0.01 g, and measured for total length in millimeters. Whole stomachs (esophagus to pyloric valve) were removed, placed in petri dishes, and frozen in

fresh water until examined. I opened each stomach and identified prey items using a dissecting microscope. At 6 to 100x magnification, all recognizable prey were identified to the lowest taxonomic level possible, depending on the condition of the stomach contents, with the help of taxonomic keys or personal communication with invertebrate specialists. Once identified, the wet weight value of each prey item was recorded to the nearest 0.0001 g.

Due to the diversity of prey consumed by both sculpin species, all identifiable prey was aggregated into nine groups based on common taxonomic characteristics for statistical comparisons. These nine groups were benthic amphipods, calanoid copepods, crabs, cumaceans, fish prey, hyperiid amphipods, polychaetes, shrimps, and "other prey" (Tables 2.A-1, 2.A-2). Benthic prey included benthic amphipods, cumaceans, and polychaetes, while pelagic prey included calanoid copepods and hyperiid amphipods. Crabs were either benthic or pelagic depending on life stage, i.e., juveniles and adult crabs were benthic and larval crabs were pelagic. Fish prey, shrimps, and "other prey" were either benthic or pelagic depending on type consumed. "Other prey" included prey that either weighed a very small amount (e.g., barnacle cyprids, harpacticoid copepods, nematodes, or ostracods, each weighing <0.0001 g) or were rare (e.g., isopods and mollusks). I removed unidentifiable tissues from the statistical comparisons because these may have been stomach lining or a variety of soft-bodied prey items. However, because both sculpin species, especially Arctic Staghorn Sculpin, had high percentages unidentifiable tissues in their stomachs, this category was kept in the descriptive analysis for both species in the Chukchi (Table 2.A-1) and Beaufort (Table 2.A-2) Seas.

All identifiable, intact prey was included in prey size versus predator size analysis. Prey was measured to the nearest 0.1 mm. Some identifiable prey was unmeasurable, thus not included in the analysis. This was most noticeable for soft-bodied prey such as polychaetes and

fishes. These prey types may have been larger than the majority of hard-bodied, identifiable prey; therefore, their non-inclusion may have downwardly-skewed the actual prey size distribution that these fishes consume in the Chukchi and Beaufort Seas.

Data analysis methods

To determine the importance of each prey item for both species sharing similar regions and depths, I used two diet indices: percent mean weight and percent occurrence. Percent mean weight was calculated as follows:

$$(2.1) \quad \%MW_i = \frac{1}{P}\sum^{j}\left[\frac{W_{ij}}{\Sigma W_{ij}}\right] \text{ x } 100$$

where $\%MW_i$ is the percent mean weight of prey type i consumed by a predator, W_{ij} is the weight of prey i in a single predator j, and ΣW_{ij} is the sum of all prey weights in the stomach of a single predator j. The sums of this calculation for each prey item over the entire sample are then divided by the number of fish with food in their stomachs (P). The resulting %MW information can be used as an indicator of the energetic importance of prey types to a fish population (Hyslop 1980; Chipps and Garvey 2007). This index has been criticized because it can overemphasize the importance of heavy prey items eaten by few predators in the population. Although there is controversy with %MW (Baker et al. 2013), this index was used in statistical comparisons because %MW is the most useful index in indicating prey energetic importance (Chipps and Garvey 2007). To accompany %MW, I calculated a second diet index, percent occurrence (%O), also known as frequency of occurrence, because it is a robust and interpretable approach (Baker et al. 2013). This method simply shows the percentage of individuals in the population that ate a specific prey type (Hyslop 1980; Baker et al. 2013). I calculated percent occurrence using the formula:

$$(2.2) \quad \%O_i = \left[\frac{O_i}{\Sigma P}\right] x\ 100$$

where $\%O_i$ is defined as the occurrence of a prey group i divided by the sum of non-empty stomachs (ΣP).

Generalist or specialist feeding strategies and the relative importance of individual prey groups to each sculpin species were determined using %MW and %O data in a graphical method which showed prey-specific abundance (PSA; Amundsen et al. 1996). Prey-specific abundance was calculated using the formula:

$$(2.3) \quad PSA_i = \left(\frac{\sum S_i}{\sum S_{ti}}\right) x\ 100$$

where prey-specific abundance (PSA_i) is the sum of the raw weight data of a specific prey group i (S_i), divided by the sum of the total stomach contents weights of only predators in the population that ate prey group i (S_{ti}). For example, calculating the PSA of crabs for Shorthorn Sculpin in the NCS region at >30 m would be the sum of all crab prey weights divided by the total stomach contents weight of all Shorthorn Sculpin in the NCS region at >30 m that consumed crabs. These PSA values are graphed with their corresponding %O values to illustrate fish feeding habits (Fig. 2.2, Amundsen et al. 1996). The resulting figure indicates the percentage of fish in a population that consumed a specific prey group, and of those fish, the percentage by weight that specific prey group contributed to their diet. Prey groups with high PSA and %O values (top-right, Fig. 2.2) show feeding specialization by the fish population, while a high PSA and low %O (top-left, Fig. 2.2) show specialization by individuals. In general, if most prey groups fall in the lower half of the figure, the species is considered a generalist, whereas if most prey groups fall in the upper half, the species is considered a specialist. The diagonal line from bottom-left to top-right indicates whether a prey group makes up a smaller proportion of the diets

of fewer individuals (bottom-left) or is dominant in the diet of the population (top-right), while the diagonal line from top-left to bottom-right gives an indication of niche breadth with more prey groups falling below this line indicating a wider niche because many groups are taken less frequently by the population. Because the "other prey" group in my analysis included many prey that weighed <0.0001 g, thus given a weight of 0 in the data set, there was no raw weight data paired with the counts data. This did not allow for an accurate PSA calculation or interpretation for the "other prey" category, but did allow for an accurate %O calculation. Therefore, for the interpretation of the "other prey" group in the PSA figures, PSA values were set to 0 and only %O was plotted. This adapted PSA method accounts for the percentage of sculpins that consumed identifiable "other prey" in all region and depth categories of the Chukchi (Table 2.A-1) and Beaufort (Table 2.A-2) Seas.

The graphical representation of niche breadth using PSA was qualitatively compared with the Levins index (Levins 1968), another measure of niche breadth. The %MW data of the nine broad prey categories were used to calculate niche breadth in the PSA figures, whereas prey counts of all identifiable taxa (Table 2.A-3) consumed by each species were used in the Levins index. Using these prey counts, the Levins index of niche breadth, B, indicated how evenly resources were used and was calculated by the following equation.

$$(2.4) \quad B = \frac{1}{\Sigma p_i^2}$$

where p_i is the proportion of sculpins consuming a prey group i. To make comparisons simpler, I used standardized Levins niche breadth, which measures niche breadth on a 0 to 1 scale, using the formula:

$$(2.5) \quad B_A = \frac{B - 1}{n - 1}$$

where B_A is the standardized niche breadth and n is the total number of unique prey types consumed by either Arctic Staghorn Sculpin or Shorthorn Sculpin in a specific region and depth category.

The sample sizes needed to adequately describe sculpin diet diversity were determined using cumulative prey curves, which plot the occurrence of novel prey eaten by a predator against a running total of examined stomachs (Chipps and Garvey 2007). When the curve is close to or at an asymptote, fish diet diversity is said to be sufficiently described (Chipps and Garvey 2007). Cumulative prey curves for both species in the SCS (Fig. 2.B-1), NCS (Fig. 2.B-2), and WBS/EBS (Fig. 2.B-3) indicated that, in some cases, a sample size of 60 fish stomachs per region and depth category was needed to fully describe sculpin diet diversity at the lowest taxonomic level. In some regions and depth categories this asymptote was never reached. The focus of the present research was to compare common, taxonomically-coarse prey groups consumed by sculpins in similar habitats. To accomplish this, the sample sizes needed per region and depth category were likely fewer than 60 stomachs. Therefore, regardless of sample size, all available sculpin stomachs, even if greater than 60, in each region and depth category of the Chukchi and Beaufort Seas were processed with results used in the statistical analysis because no formal diet comparisons exist for these species in the western Arctic.

A multivariate technique was used to simultaneously evaluate differences in prey proportions (Chipps and Garvey 2007) in Arctic Staghorn Sculpin and Shorthorn Sculpin diets between sea-regions and depths. The assumptions of parametric multivariate analysis of variance (MANOVA) are strict and oftentimes not met when using diet composition data (Chipps and Garvey 2007). Diet data sets often contain a multitude of zeroes, which make it difficult to meet distributional assumptions (Quinn and Keough 2002). Because of these issues, I used a

permutation-based version of MANOVA based on a Bray-Curtis distance matrix using the function *adonis* (i.e., non-parametric MANOVA, hereafter NP MANOVA) in the vegan package of R, version 2.15.2. This method is considered to be a robust alternative to parametric MANOVA and parametric ordination methods (Legendre and Anderson 1999). The output of this method is a pseudo-*F* statistic analogous to that of MANOVA. Using the %MW data of the nine prey categories, I developed a NP MANOVA model that simultaneously compared the diet compositions of Arctic Staghorn Sculpin and Shorthorn Sculpin within a region and depth category. I used this model to evaluate my hypothesis of a significant, interspecific difference in diets between Arctic Staghorn Sculpin and Shorthorn Sculpin throughout my study regions and depth categories.

To better understand how the morphological differences between these sculpin species might lead to differences in their diets, I examined mouth gape width and height measurements. Using digital calipers, measurements were made to the nearest 0.1 mm. Gape width was defined as the greatest distance between the corners of both jaws, while gape height was defined as the greatest distance between the top and bottom of the mouth (Scharf et al. 2000). The resulting measurements were meant to represent the maximum size dimensions of prey a fish could eat at a given body size. Using simple linear regression, the gape measurements were regressed against total length (R commander, version 1.9–6). If total length was found to be a significant predictor of gape width or height, the slopes were compared between species using paired t-tests to determine interspecific differences in mouth morphologies.

The results from the mouth morphology analysis were then qualitatively compared to a quantile regression analysis used to determine the relationship between sculpin body length and the size of prey consumed. Quantile regression minimizes the sums of the absolute values of

residuals to fit lines at specified quantiles ranging from 0 to 100 (Scharf et al. 1998; Scharf et al. 2000). I used this method to fit lines at the 10^{th}, 50^{th}, and 90^{th} quantiles to determine the size ranges of prey consumed by Arctic Staghorn Sculpin and Shorthorn Sculpin at a given body length. All quantile regressions were conducted using the quantreg package in R, version 3.1.0. By comparing the two methods, it was possible to relate the size ranges of prey consumed by both sculpins at a given body length to any differences in sculpin mouth morphologies at that given body length.

Results

A total of 392 Arctic Staghorn Sculpin and 352 Shorthorn Sculpin with identifiable prey in their stomachs were analyzed to compare their diets within regions and depths of the Chukchi and Beaufort Seas. Despite sharing some prey groups, NP MANOVA indicated significant, interspecific differences in sculpin diet compositions in all sea-region and depth categories examined in this study ($F= 6.543–31.045$; $p<0.001$). Arctic Staghorn Sculpin exclusively consumed benthic prey, especially benthic amphipods and polychaetes, throughout all regions and depths of the Chukchi (Fig. 2.3; Table 2.A-1) and Beaufort Seas (Fig. 2.4; Table 2.A-2). Shorthorn Sculpin consumed a more varied diet that included some pelagic prey, depending on the region they inhabited. In the SCS and NCS regions, Shorthorn Sculpin consumed mostly benthic prey, including benthic amphipods, crabs, fish prey, and shrimps (Fig. 2.3; Table 2.A-1), but WBS and EBS conspecifics consumed a more pelagic diet, consisting of comparatively higher proportions of hyperiid amphipods and pelagic stages of crabs (Fig. 2.4; Table 2.A-2). Similarities between Arctic Staghorn Sculpin and Shorthorn Sculpin diets were most noticeable in the NCS region (Fig. 2.3), with both species consuming high proportions of benthic amphipods.

On average, Shorthorn Sculpin used for this research were larger in body size than Arctic Staghorn Sculpin. This was true for sculpins collected by the PSBT and otter trawls (Table 2.A-4) and those used for stomach contents analysis (Fig. 2.5). Additionally, the mean lengths of each species collected (Table 2.A-4) and used in stomach contents analysis (Fig. 2.5) were smaller in the Beaufort Sea than in the Chukchi Sea.

The PSA figures for the SCS (Fig. 2.6), NCS (Fig. 2.7), and WBS/EBS (Fig. 2.8) showed that Arctic Staghorn Sculpin and Shorthorn Sculpin were mostly generalists with some prey types being dominant depending on the specific region and depth category. Overall, each sculpin species used prey resources differently within all regions and depth categories, with no one prey type dominating the diet of either species in a shared area. In terms of dominant prey types, benthic amphipods dominated Arctic Staghorn Sculpin diet in the SCS at ≤30 m depths (Fig. 2.6), with no other dominant prey consumed by either species in this region regardless of depth. In both depth categories of the NCS region, benthic amphipods again dominated Arctic Staghorn Sculpin diet (Fig. 2.7). Relative to all other regions, Shorthorn Sculpin consumed higher amounts of benthic amphipods in the NCS, but no prey dominated their diet (Fig. 2.7). In both depth categories of the WBS region (Fig. 2.8), benthic amphipods dominated Arctic Staghorn Sculpin diet, while hyperiid amphipods dominated the diet of Shorthorn Sculpin. In the EBS region (Fig. 2.8), polychaetes dominated the diets of Arctic Staghorn Sculpin, with no dominant prey in Shorthorn Sculpin diet.

A smaller Levins niche breadth value (Fig. 2.5) corresponded to a dominant, or nearly dominant, prey group in the PSA figures (Figs. 2.6, 2.7, 2.8). Both methods indicated Shorthorn Sculpin had a more varied diet and wider niche breadth than Arctic Staghorn Sculpin in both depths of the SCS and NCS regions and in the EBS at ≤30 m depth (Fig. 2.5). This pattern was

reversed in both depths of the WBS region (Fig. 2.5), with Arctic Staghorn Sculpin having a more varied diet and wider niche breadth.

Analyses of each sculpins' body size and mouth morphology characteristics revealed differences between the two species. Simple linear regression showed fish body length to be a significant predictor of both gape width (Fig. 2.9) and gape height (Fig. 2.10) for Arctic Staghorn Sculpin and Shorthorn Sculpin. Subsequent analysis of the regression slopes using paired t-tests showed Shorthorn Sculpin gape width ($df=49$, $t=11.870$, $p<0.001$) and height ($df=49$, $t=12.628$, $p<0.001$) were significantly greater at a given total length value than that of Arctic Staghorn Sculpin.

Because a large number of prey length measurements were needed to conduct quantile regression analysis for both sculpin species, I pooled all information available from both seas and assumed same-species and same-size fishes consumed a similar prey size spectrum throughout their distributions. The fitted quantile regressions indicated that fish body length was a significant predictor of the size of prey consumed by Arctic Staghorn Sculpin (Fig. 2.11) at the 10^{th} ($t=2.362$, $p=0.018$), 50^{th} ($t=13.748$, $p<0.001$), and 90^{th} quantiles ($t=10.319$, $p<0.001$) and of the size of prey consumed by Shorthorn Sculpin (Fig. 2.12) at the 10^{th} ($t=3.042$, $p=0.002$), 50^{th} ($t=4.746$, $p<0.001$), and 90^{th} quantiles ($t=7.886$, $p<0.001$). The slopes of the lines at each quantile indicated that at similar body sizes, Arctic Staghorn Sculpin and Shorthorn Sculpin consumed different sizes of prey, with Shorthorn Sculpin consuming larger prey at the 90^{th} and 10^{th} quantiles, and Arctic Staghorn Sculpin consuming larger prey at the 50^{th} quantile (Fig. 2.13).

Discussion

Throughout their distributions in the Chukchi and Beaufort Seas, Arctic Staghorn Sculpin and Shorthorn Sculpin partition prey within shared habitats by consuming different proportions

of similar prey types or by consuming different prey types all together. Previous accounts of these species' feeding habits indicate the benthic generalist nature of Arctic Staghorn Sculpin in the Bering (Cui et al. 2012), Chukchi (Coyle et al. 1997), and Beaufort Seas (Atkinson and Percy 1992) and Shorthorn Sculpin in the Bering (Cui et al. 2012), Labrador (Moore and Moore 1974; Atkinson and Percy 1992) and Baltic Seas (Cardinale et al. 2000). My research agrees with these previous assessments that both species are generalists. There may be a variety of reasons why these species partition prey; possibilities considered here are the effects of habitat-related processes on diet composition and size-related morphological differences.

Although sculpin diets were different from one another in every habitat, there were some similarities in the Chukchi Sea, especially in the NCS region. Both sculpin's diets were composed of more unique benthic taxa in the Chukchi Sea compared to the Beaufort Sea. This was expected given that areas of the Chukchi Sea are documented as more benthically productive (Grebmeier et al. 2006; Blanchard et al. 2013; Blanchard and Feder 2014) than those in the Beaufort Sea (Carey and Ruff 1977; Carey 1987; Carey 1991). In the NCS region, both sculpins consumed appreciable amounts of benthic amphipods. The abundance and availability of these macroinvertebrates (Blanchard and Feder 2014) in the NCS may have been driven in part by some broad oceanographic-related habitat characteristics of the region. One such process is the presence of a semi-permanent, bottom-water front located near Point Franklin (Weingartner 1997) which supports a high abundance of benthic taxa near the frontal boundary (Feder et al. 1994b; Dunton et al. 2005). Other contributing factors may have included enhanced organic carbon deposition in the NCS near Hanna Shoal and Barrow Canyon, the results of which could have increased food availability to benthic macroinvertebrate communities (Blanchard et al. 2013; Blanchard and Feder 2014). Each of these processes may have increased the amount of

benthic amphipods available for sculpins in the NCS region. This study suggests that locally-abundant prey groups can cause the normally different diets of both sculpins to be more similar to one another.

In addition to habitat characteristics, body length and morphology-related processes are responsible for prey partitioning between the two sculpins in shared habitats. Shorthorn Sculpin in this analysis were on average larger than Arctic Staghorn Sculpin. This could be an artifact of gear selectivity, however, Shorthorn Sculpin attain a larger length, usually <350 mm, than Arctic Staghorn Sculpin, usually <150 mm (Mecklenburg et al. 2002). For both species, a larger body length was related to greater mouth gape dimensions, which were directly related to the size of prey a fish could consume (Keast and Webb 1966; Juanes et al. 2002). At similar body lengths, Shorthorn Sculpin have larger gapes and thus can consume same-size and larger prey than Arctic Staghorn Sculpin. This allows Shorthorn Sculpin access to prey Arctic Staghorn Sculpin cannot consume; which accounts for the wider niche breadth of Shorthorn Sculpin. Theoretically, Shorthorn Sculpin could consume a nearly identical diet as Arctic Staghorn Sculpin; however, their diets were very different. These differences were driven in part by species-specific, differences in mouth morphologies, which may be an important mechanism in reducing diet similarities between other Arctic marine fishes as well.

Arctic Staghorn Sculpin and Shorthorn Sculpin were expected to consume a primarily benthic diet throughout ontogeny; this was not always the case for Shorthorn Sculpin. Fish diets can vary greatly with ontogeny (Chipps and Garvey 2007) in both size (Labropoulou and Eleftheriou 1997) and type (Werner and Gilliam 1984) of prey consumed. Considering prey types, Arctic Staghorn Sculpin consumed benthic prey in all habitats while small, i.e., ≤60 mm, Shorthorn Sculpin frequently consumed pelagic prey in SCS and Beaufort Sea habitats. It is not

unheard of for sculpins to eat pelagic prey; the Ribbed Sculpin (*Triglops pingelli*) is known to consume pelagic zooplankton in the Canadian Beaufort Sea (Atkinson and Percy 1992). It is possible that both the Ribbed and Shorthorn Sculpin exhibit this type of feeding behavior as a means of resource partitioning throughout ontogenetic stages as to not compete with other confamilial sculpins.

This study suggests that the present Chukchi Sea food web model parameters, which were based on Bering Sea fish diet compositions, may be acceptable for Arctic Staghorn Sculpin but should be reevaluated for Shorthorn Sculpin. In the model, Arctic Staghorn Sculpin was included in an "other sculpins" functional group along with 10 sculpin genera, including *Artediellus, Blepsias, Enophrys, Gymnocanthus, Icelus, Megalocottus, Microcottus, Nautichthys,* and *Triglops* (Whitehouse 2013). This model was parameterized with benthic amphipods and polychaetes composing >80% of these fishes' diets. When accounting for identifiable prey, Arctic Staghorn Sculpin diet composition in my study was quite similar to that used in the model. Benthic amphipods and polychaetes composed about 81% of its diet in the Chukchi Sea and 72% of its diet in the Beaufort Sea. This suggests that Arctic Staghorn Sculpin diet could be similar throughout the Arctic and that using proxy diet composition could adequately model this species' feeding habits. Shorthorn Sculpin was included in the "large-mouth sculpin" functional group along with two other species belonging to the genera *Myoxocephalus* and *Hemilepidotus* (Whitehouse 2013). Diet composition of Shorthorn Sculpin in the present research did not agree as well with the data used in the model. Shorthorn Sculpin in the Bering Sea was characterized as a heavy consumer (>80% of diet composition) of Snow Crab (*Chionocetes opilio*) and other crabs, with shrimps and benthic amphipods composing only ~2.5 to 4% of the diet (Whitehouse 2013). My study indicates that the present model would overemphasize the importance of snow

crabs and other crabs by 50 to 70% throughout the Chukchi and Beaufort Sea habitats considered here. Consequently, the importance of shrimps, benthic amphipods, and hyperiid amphipods would be undervalued in both seas. Therefore, to adequately model the effects of Shorthorn Sculpin on prey populations, both the benthic and pelagic components of its diet should be considered, which could be accomplished by taking into account region- and body size-based diet variability.

In conclusion, this study documents sculpin diet variability due to habitat and species-specific morphological differences. While it is true that both sculpins act primarily as generalist benthivores, this is not always the case for the Shorthorn Sculpin in the Chukchi and Beaufort Seas, which occasionally functions as a pelagivore. Without accounting for species' diets on a region and size basis, these patterns of prey consumption would likely have been hidden due to prey taxa and prey weights being averaged over a larger sample size and spatial scale. Therefore, a coarse analysis that does not account for regional and morphological differences could bias food web models by underestimating or overestimating the effects fishes have as predators on benthic or pelagic prey resources. As future ecosystem models are developed for the Arctic, finer-scaled diet analyses such as the present study will be needed to account for variability in fish species' diets.

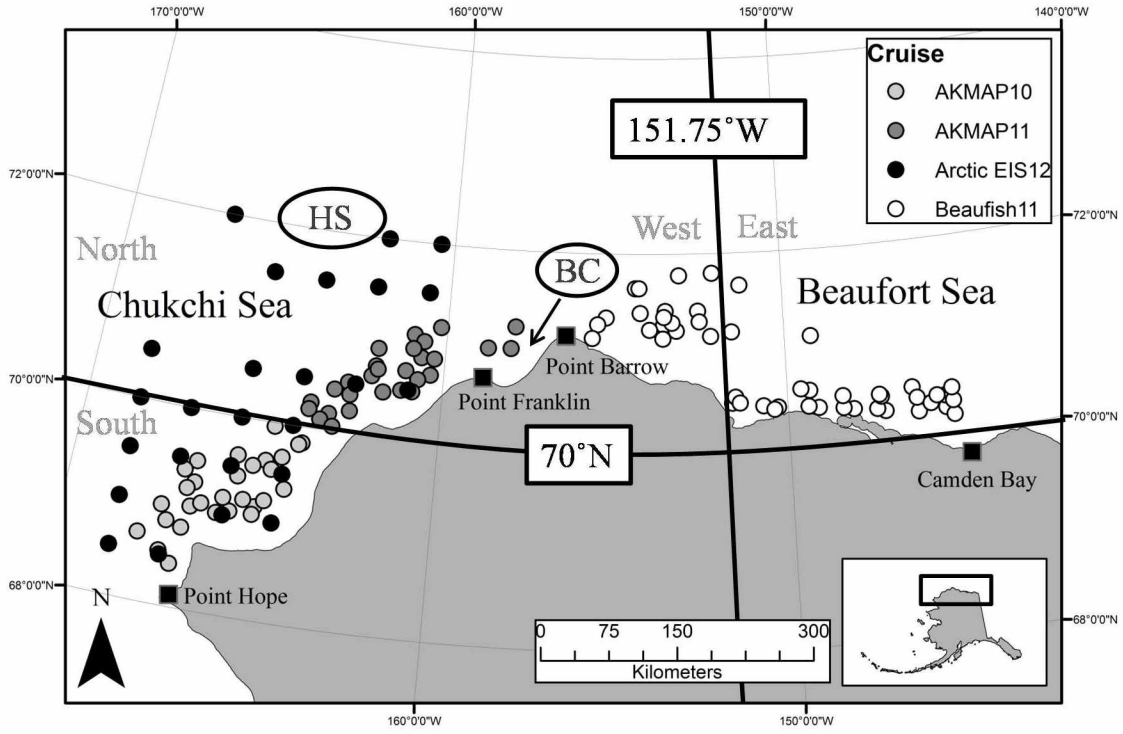

Fig. 2.1 Stations sampled in the Chukchi and Beaufort Seas. Each point on the map represents a station where Arctic Staghorn Sculpin or Shorthorn Sculpin were collected for stomach contents analysis. Fishes were taken over three Chukchi Sea cruises (AKMAP10–11 and Arctic EIS12) and one Beaufort Sea cruise (Beaufish11). North and south Chukchi Sea regions were divided at 70°N, while west and east Beaufort Sea regions were divided at 151.75°W. The approximate positions of Hanna Shoal and Barrow Canyon are denoted as "HS" and "BC," respectively.

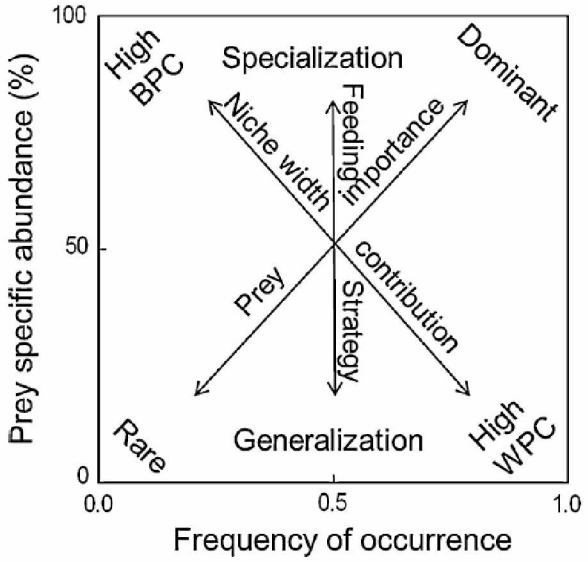

Fig. 2.2 Explanation of the prey-specific abundance versus frequency of occurrence (also known as %O) graphical method used to visualize fish feeding strategies. BPC refers to between-phenotype component, while WPC refers to within-phenotype component. Figure adapted from Amundsen et al. (1996).

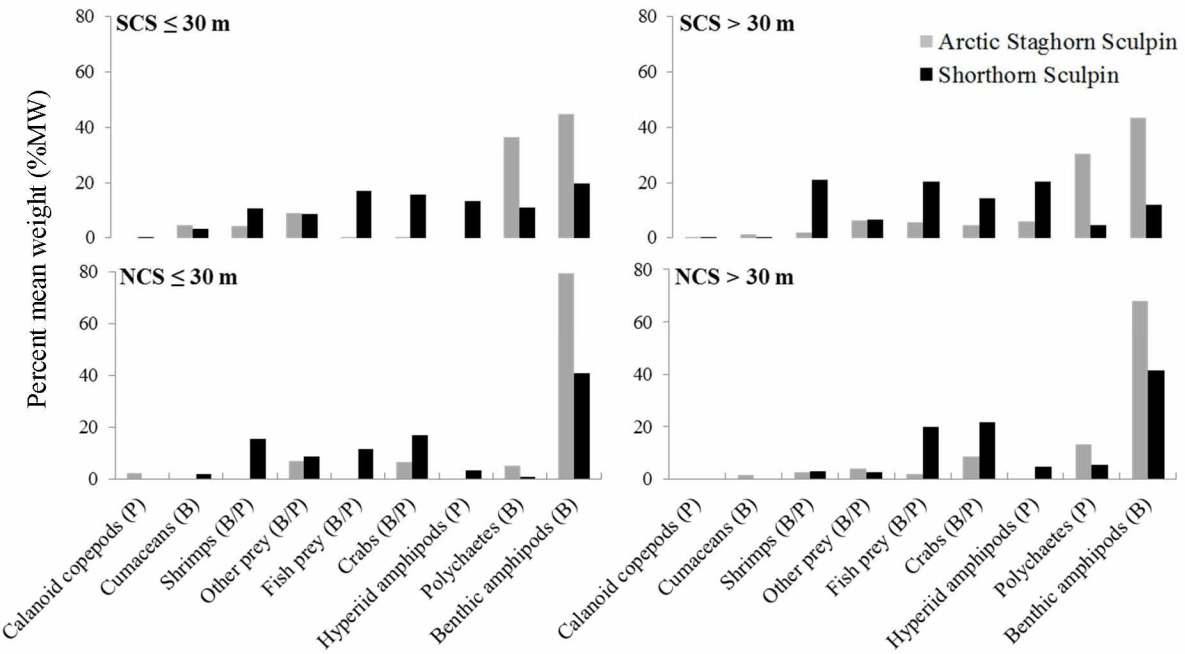

Fig. 2.3 Percent mean weight (%MW) of Arctic Staghorn Sculpin and Shorthorn Sculpin diets in the Chukchi Sea summarized by two regions, south and north Chukchi Sea (SCS and NCS, respectively) and two depth categories (≤30 m and >30 m). Prey categories along the x-axis were ranked by the combined amount of biomass a prey category contributed to both sculpin's diets, from left (least) to right (most). A "B" or "P" next to a prey item signifies whether that prey is benthic or pelagic.

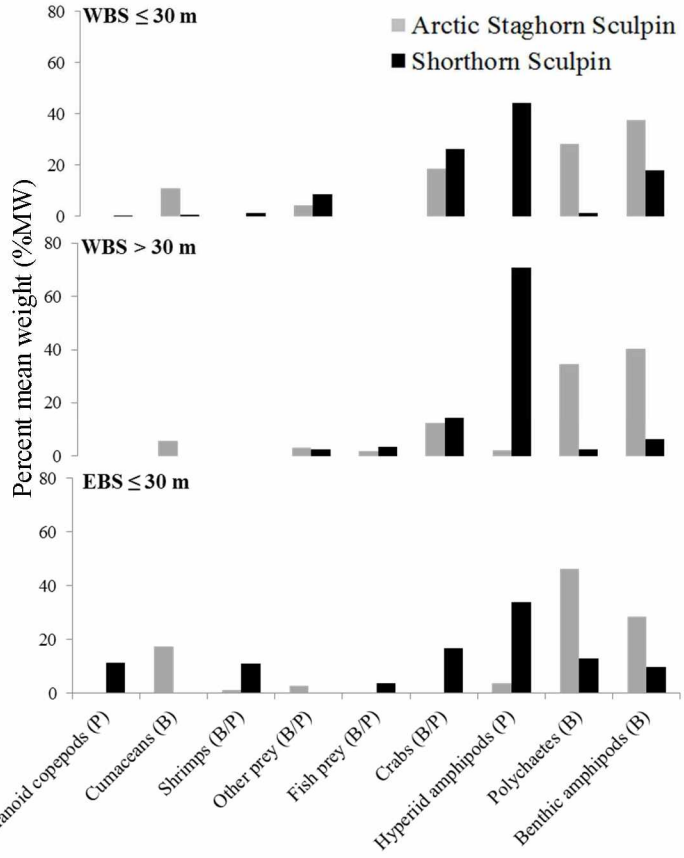

Fig. 2.4 Percent mean weight (%MW) of Arctic Staghorn Sculpin and Shorthorn Sculpin diets in the Beaufort Sea summarized by two regions, east and west Beaufort Sea (WBS and EBS, respectively) and two depth categories (≤30 m and >30 m). Prey categories along the x-axis were ranked by the combined amount of biomass a prey category contributed to both sculpin's diets, from left (least) to right (most). A "B" or "P" next to a prey item signifies whether that prey is benthic or pelagic.

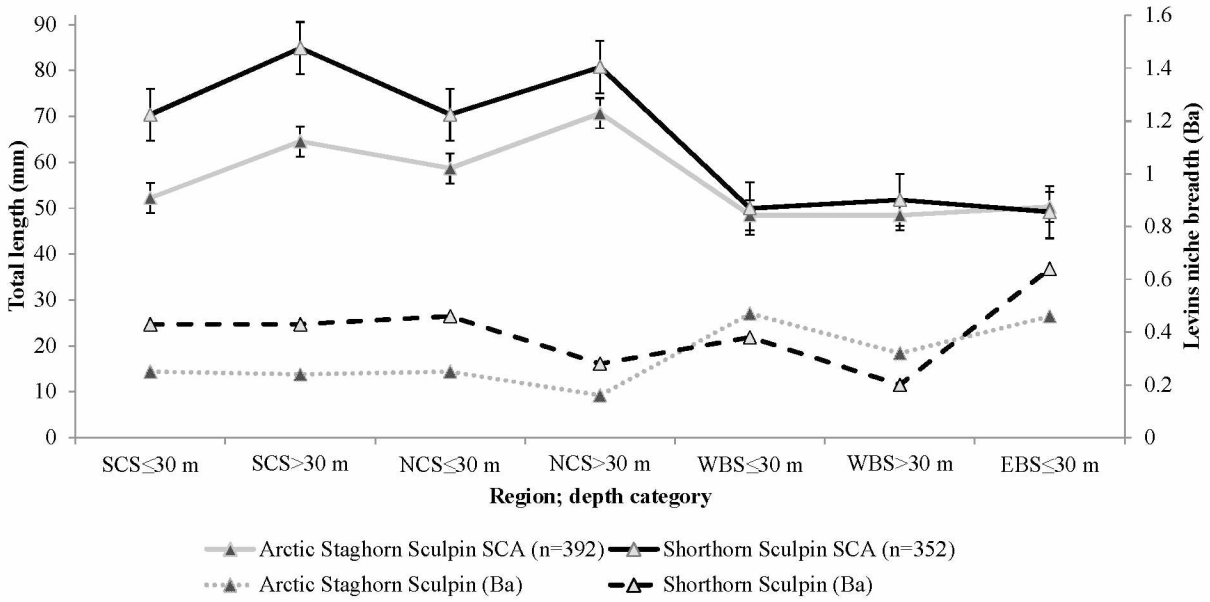

Fig. 2.5 Size distribution (solid lines) of Arctic Staghorn Sculpin and Shorthorn Sculpin used for stomach contents analysis (SCA), and their corresponding Levins niche breadth index values (Ba; dashed lines) within two depth categories, (≤30 m and > 30 m) of two Chukchi Sea regions: south Chukchi (SCS) north Chukchi (NCS), and two Beaufort Sea regions: west Beaufort (WBS), and east Beaufort (EBS). Error bars for the sculpin size distribution lines indicate the standard error of the mean fish size within a region and depth category.

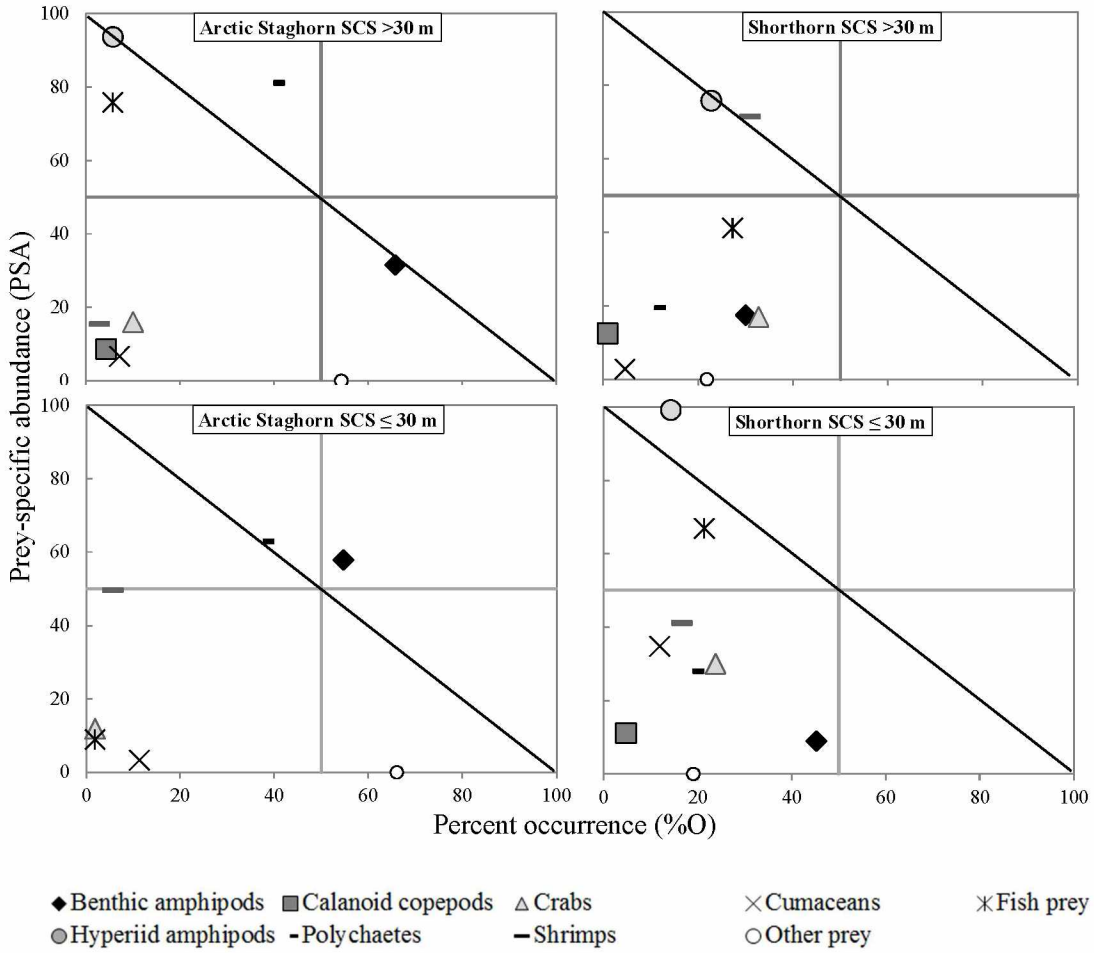

Fig. 2.6 Prey-specific abundance for Arctic Staghorn Sculpin and Shorthorn Sculpin in the south Chukchi Sea region (SCS) at both ≤30 m and >30 m depths. Diagonal lines from top-left to bottom-right represent population niche breadth as detailed in Fig. 2.2. In general, more prey items falling below the line signifies a wider niche breadth and more generalized diet, while more prey items above the line signifies a narrower niche breadth and more specialized diet.

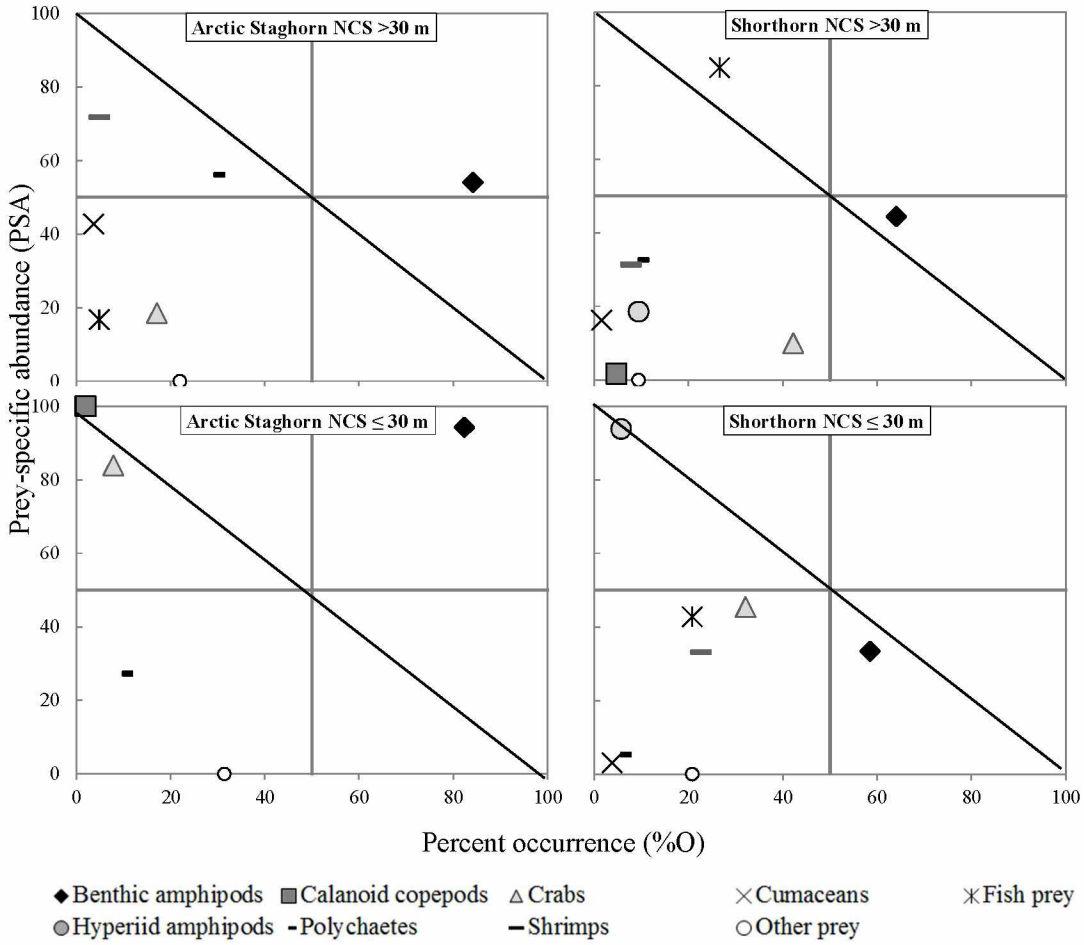

Fig. 2.7 Prey-specific abundance for Arctic Staghorn Sculpin and Shorthorn Sculpin in the north Chukchi Sea region (NCS) at ≤30 m and >30 m depths. Diagonal lines from top-left to bottom-right represent population niche breadth as detailed in Fig. 2.2. In general, more prey items falling below the line signifies a wider niche breadth and more generalized diet, while more prey items above the line signifies a narrower niche breadth and more specialized diet.

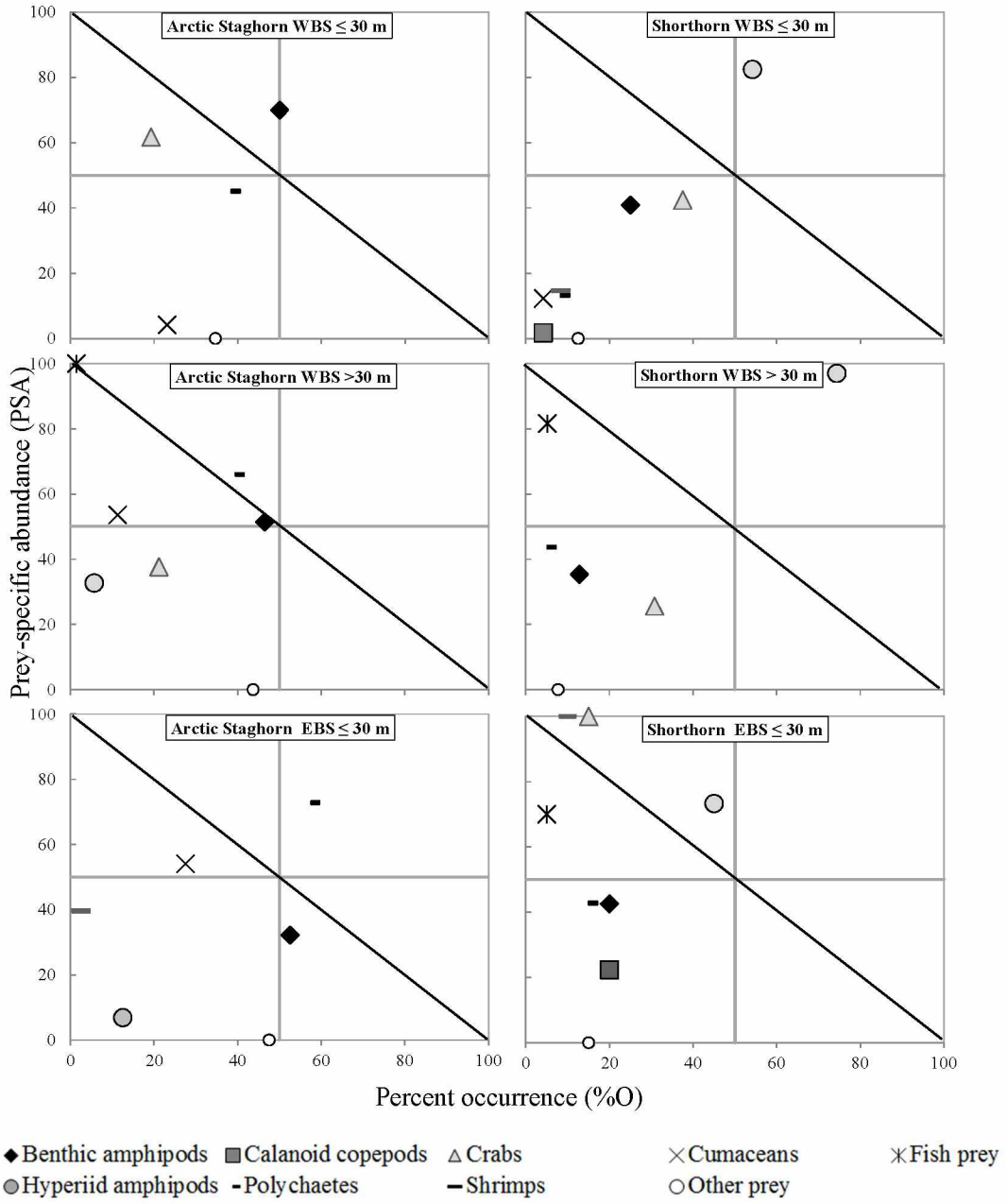

Fig. 2.8 Prey-specific abundance for Arctic Staghorn Sculpin and Shorthorn Sculpin in the west Beaufort Sea region (WBS) at ≤30 m and >30 m depths and the east Beaufort Sea region (EBS) at ≤30 m. Diagonal lines from top-left to bottom-right represent population niche breadth as detailed in Fig. 2.2. In general, more prey items falling below the line signifies a wider niche breadth and more generalized diet, while more prey items above the line signifies a narrower niche breadth and more specialized diet.

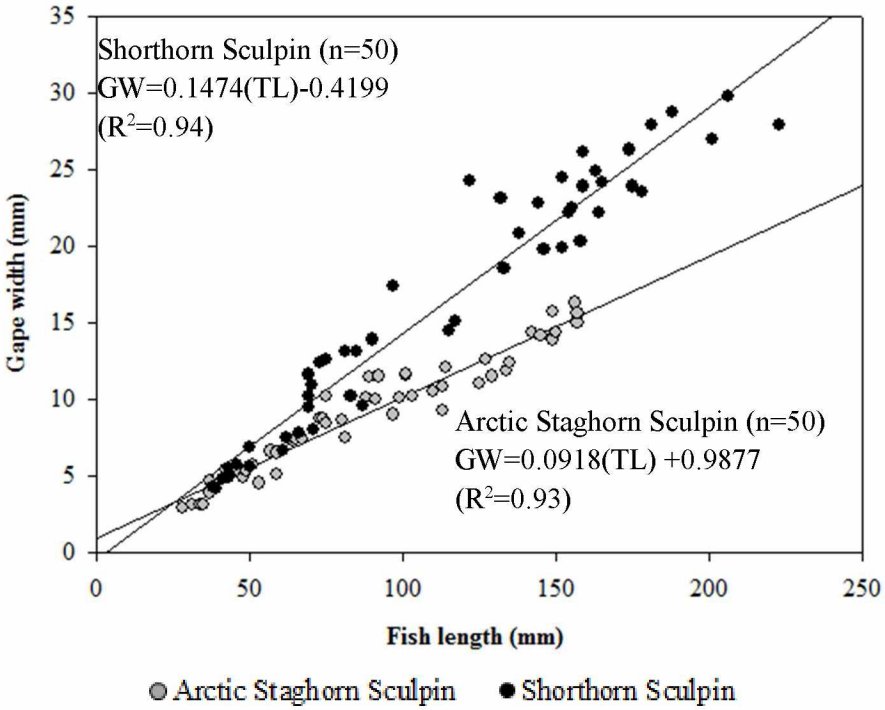

Fig. 2.9 Gape width (GW) regressed against fish total length (TL) for Arctic Staghorn Sculpin and Shorthorn Sculpin.

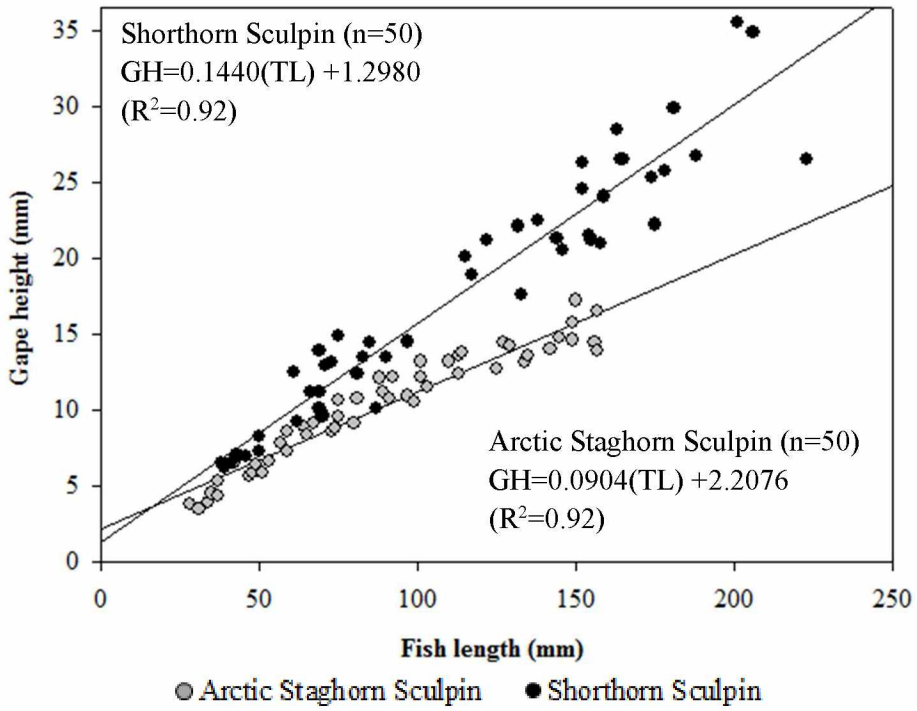

Fig. 2.10 Gape height (GH) regressed against fish total length (TL) for Arctic Staghorn Sculpin and Shorthorn Sculpin.

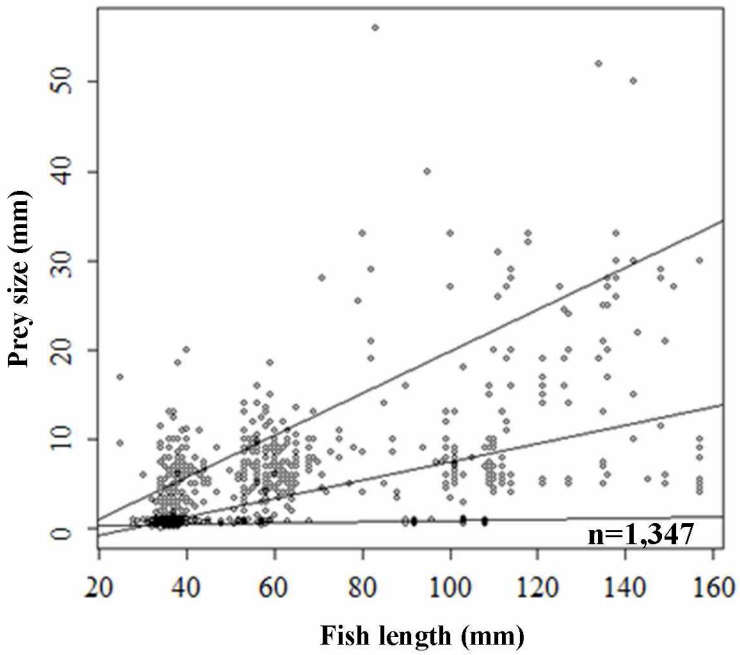

Fig. 2.11 Regression plot of the 10th, 50th, and 90th quantiles, highlighting the size ranges of prey consumed by Arctic Staghorn Sculpin in both the Chukchi and Beaufort Seas at a given total length value.

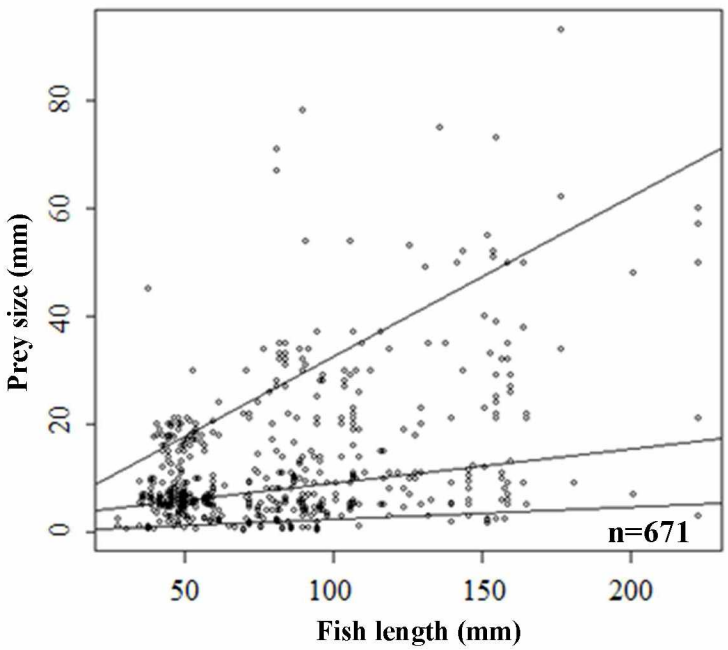

Fig. 2.12 Regression plot of the 10th, 50th, and 90th quantiles, highlighting the size ranges of prey consumed by Shorthorn Sculpin in both the Chukchi and Beaufort Seas at a given total length value.

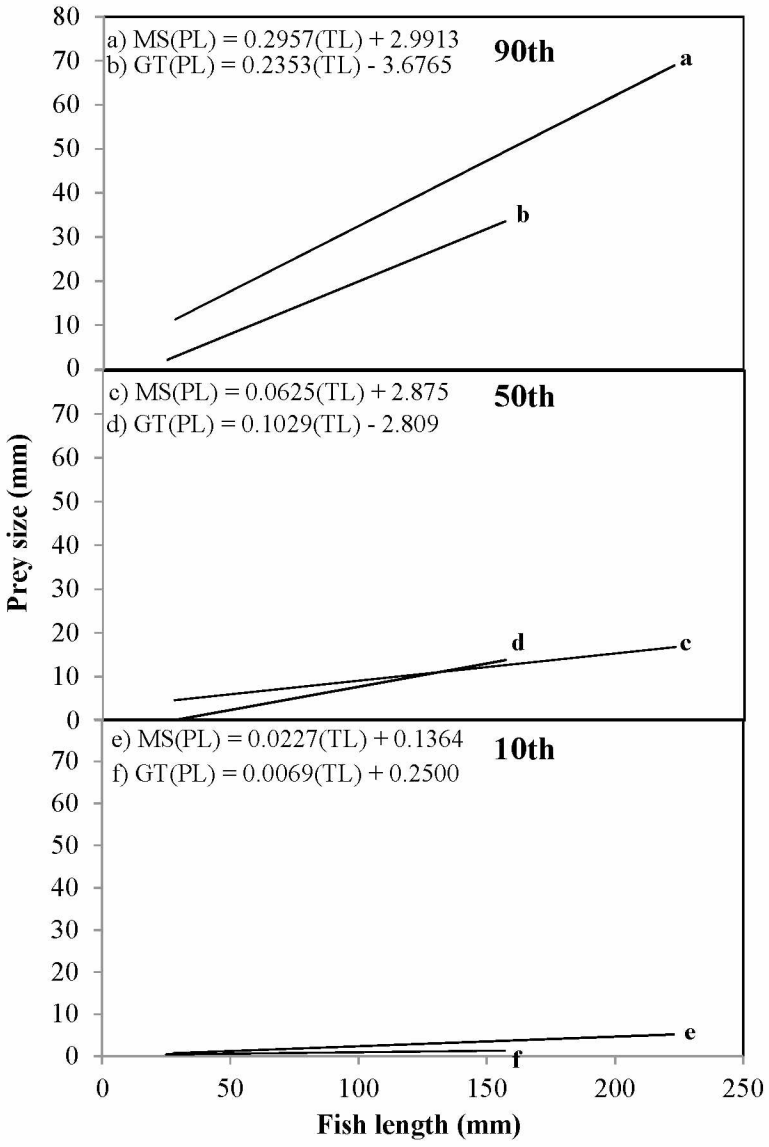

Fig. 2.13 Comparison of the quantile regression slopes of the sizes of prey consumed by Arctic Staghorn Sculpin and Shorthorn Sculpin at the 10^{th}, 50^{th}, and 90^{th} quantiles. Regression equations are listed for each species and quantile (a-f). Abbreviations in the regression equations are as follows: GT=*G. tricuspis* (Arctic Staghorn Sculpin), MS=*M. Scorpius* (Shorthorn Sculpin), PL= prey length, and TL=fish total length.

Appendix 2.A

Sculpin diet compositions and body size distributions

Table 2.A-1 Arctic Staghorn Sculpin and Shorthorn Sculpin diets summarized by %MW and %O in two depth categories (≤30 m and >30m) of the south and north Chukchi Sea regions (SCS and NCS, respectively). Because "unknown" prey was common, it was included here. Total number of prey, total prey weight (g), and total stomachs are listed at the end of the table.

	SCS ≤30 m %MW (%O)		SCS >30 m %MW (%O)		NCS ≤30 m %MW (%O)		NCS >30 m %MW (%O)	
Prey categories	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin
Benthic amphipods	**18.7 (48)**	**15.6 (37)**	**27.0 (63)**	**10.1 (29)**	**74.4 (74)**	**40.2 (57)**	**61.6 (78)**	**39.6 (60)**
Anonyx spp.	1.4 (2)	–	0.5 (1)	0.3 (1)	2.1 (4)	–	2.8 (6)	0.3 (1)
Atylus collingi	–	–	–	–	5.5 (5)	–	<0.1 (1)	1.4 (1)
Erichthonius spp.	–	–	0.9 (3)	0.1 (1)	0.3 (2)	–	<0.1 (1)	0.2 (1)
Ischyocerus spp.	–	–	–	0.9 (1)	29 (30)	17.3 (20)	2.5 (3)	2.1 (3)
Maera spp.	–	<0.1 (2)	–	0.4 (1)	–	–	0.1 (2)	0.7 (1)
Melita spp.	2.0 (3)	4.8 (12)	6.9 (15)	5.3 (11)	4.1 (5)	0.5 (2)	4.7 (9)	3.4 (9)
Photis spp.	0.7 (3)	–	<0.1 (1)	–	–	–	2.3 (3)	1.2 (3)
Protomedeia spp.	5.8 (10)	<0.1 (2)	0.9 (4)	0.1 (2)	–	–	12.6 (26)	5.9 (15)
Ampelescidae	0.9 (2)	0.5 (2)	0.3 (1)	0.2 (1)	0.1 (2)	4.4 (9)	1.7 (6)	1.0 (3)
Ampithoidae	–	–	–	<0.1 (1)	–	–	0.5 (2)	–
Corophiidae	<0.1 (2)	<0.1 (2)	–	<0.1 (1)	–	–	0.6 (1)	–
Eusiridae	–	–	–	<0.1 (1)	–	–	0.1 (1)	1.6 (3)
Lysianassidae	0.1 (2)	–	–	–	–	0.2 (2)	0.2 (3)	–
Oedicerotidae	1.9 (3)	0.3 (2)	1.1 (11)	0.9 (3)	1.7 (2)	2.5 (6)	2.5 (7)	0.6 (1)
Phoxocephalidae	–	–	<0.1 (1)	–	–	0.4 (4)	1.0 (3)	0.1 (1)
Pleustidae	–	–	–	–	–	1.8 (6)	–	–
Stenothoidae	–	–	1.1 (5)	0.5 (2)	–	–	–	–
Synopiidae	–	–	–	–	–	–	<0.1 (1)	1.2 (6)
Unid. benthic amphipods	6.0 (33)	10.0 (24)	15.2 (41)	1.6 (11)	31.5 (39)	13.2 (24)	30.1 (54)	19.9 (44)
Calanoid copepods	**<0.1 (12)**	**0.2 (4)**	**0.2 (4)**	**0.1 (1)**	**2.1 (2)**	**–**	**–**	**0.2 (4)**
Crabs	**0.2 (2)**	**12.6 (20)**	**2.6 (10)**	**12.7 (31)**	**6.2 (7)**	**16.9 (31)**	**8.3 (16)**	**20.6 (40)**
Chionocetes opilio zoea	–	–	–	0.2 (1)	–	<0.1 (2)	–	–
Chionocetes opilio meg.	–	–	–	0.7 (3)	–	2.2 (11)	–	1.3 (6)
Chionocetes opilio juv.	–	–	–	0.4 (3)	–	–	–	0.4 (1)
Hyas coarctatus meg.	–	–	–	0.9 (1)	–	1.4 (6)	1.1 (1)	0.1 (1)
Hyas coarctatus juv.	–	–	–	2.5 (5)	–	–	1.2 (2)	0.2 (3)
Paguridae zoea	–	2.2 (4)	<0.1 (1)	1.6 (5)	–	<0.1 (2)	–	1.5 (3)
Paguridae juv.	–	2.1 (2)	0.2 (1)	2.9 (11)	2.1 (2)	3.6 (13)	3.2 (9)	5.8 (18)
Telmessus cheiragonus meg.	–	–	0.2 (1)	1.2 (3)	–	–	–	–
Telmessus cheiragonus juv.	0.2 (2)	7.7 (14)	0.2 (1)	0.5 (3)	1.8 (2)	2.4 (7)	–	0.1 (1)
Unid. Crabs	–	0.6 (2)	2.1 (4)	1.8 (7)	2.3 (4)	7.2 (17)	2.7 (4)	11.2 (21)
Cumaceans	**2.2 (10)**	**2.7 (10)**	**1.1 (7)**	**0.1 (4)**	**–**	**2.0 (4)**	**1.3 (3)**	**0.2 (1)**
Diastylidae	0.7 (3)	0.5 (2)	–	–	–	2.0 (2)	1.2 (1)	0.2 (1)
Leuconidae	1.3 (2)	<0.1 (2)	1.1 (4)	0.1 (3)	–	–	0.1 (1)	–
Nannastacidae	<0.1 (2)	<0.1 (2)	<0.1 (1)	–	–	<0.1 (2)	–	–
Unid. cumaceans	0.3 (3)	2.2 (4)	<0.1 (3)	<0.1 (1)	–	<0.1 (2)	0.1 (1)	–
Fish prey	**0.2 (2)**	**13.7 (18)**	**4.8 (5)**	**19.7 (26)**	**–**	**11.6 (20)**	**1.6 (4)**	**19.5 (25)**
Ammodytes hexapterus	–	–	–	–	–	–	–	1.5 (1)
Boreogadus saida	–	–	–	–	–	–	–	0.5 (1)
Gymnocanthus tricuspis	–	1.4 (2)	–	7.9 (10)	–	–	–	8.8 (12)
Ulcina olrikii	–	–	–	1.0 (2)	–	–	–	–
Cottidae	0.2 (2)	1.4 (2)	1.4 (1)	2.8 (3)	–	1.2 (6)	–	0.4 (1)
Liparidae	–	–	–	–	–	–	–	0.5 (3)
Pleuronectidae	–	–	–	0.9 (1)	–	–	–	–
Stichaeidae	–	–	1.4 (1)	0.3 (2)	–	4.6 (6)	–	0.7 (3)
Zoarcidae	–	–	–	–	–	–	–	0.2 (1)

Table 2.A-1 continued Arctic Staghorn Sculpin and Shorthorn Sculpin diet summary within the Chukchi Sea.

	SCS ≤30 m MW (%O)		SCS >30 m %MW (%O)		NCS ≤30 m %MW (%O)		NCS >30 m %MW (%O)	
Prey categories	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin
Hyperiid amphipods	**–**	**9.8 (12)**	**4.4 (5)**	**19.7 (22)**	**–**	**3.4 (6)**	**–**	**4.5 (9)**
Hyperia spp.	–	–	–	0.1 (1)	–	–	–	–
Themisto libellula	–	5.2 (6)	2.9 (4)	16 (17)	–	3.4 (4)	–	3.2 (4)
Themisto spp.	–	2.6 (4)	1.4 (1)	1.3 (3)	–	<0.1 (2)	–	1.3 (4)
Unid. hyperiid amphipods	–	2.0 (2)	–	2.2 (3)	–	–	–	–
Polychaetes	**27.0 (33)**	**9.0 (16)**	**24.3 (38)**	**4.2 (10)**	**5.1 (9)**	**1.0 (6)**	**12.7 (27)**	**5.5 (9)**
Nephtys spp.	–	–	1.4 (1)	–	–	–	0.3 (1)	–
Ampharetidae	–	–	–	–	1.2 (2)	–	–	–
Glyceridae	–	2.1 (2)	–	–	–	–	–	–
Lumbrineridae	–	–	0.7 (1)	–	–	–	0.1 (1)	–
Maldonidae	–	–	–	–	–	–	0.7 (1)	–
Phyllodocidae	–	–	–	–	–	–	0.3 (2)	–
Polynoidae	0.9 (2)	–	4.7 (5)	<0.1 (1)	0.5 (2)	0.2 (2)	4.5 (8)	–
Unid. polychaetes	26.1 (32)	6.9 (14)	17.5 (32)	4.2 (10)	3.4 (7)	0.8 (4)	6.9 (18)	5.5 (9)
Shrimps	**3.3 (5)**	**8.7 (14)**	**1.6 (3)**	**20.1 (30)**	**–**	**15.2 (22)**	**2.4 (4)**	**3.0 (7)**
Argis spp.	1.9 (2)	3.3 (6)	0.2 (1)	4.4 (7)	–	5.5 (9)	1.9 (2)	1.4 (3)
Eualus spp.	–	1.6 (2)	–	2.8 (4)	–	–	–	1.1 (3)
Crangonidae	–	1.7 (4)	–	0.6 (3)	–	4.3 (6)	–	–
Hippolytidae	–	–	–	1.3 (3)	–	–	–	0.2 (1)
Pandalidae	1.4 (3)	–	–	4.2 (9)	–	1.2 (2)	–	–
Unid. Shrimps	–	2.1 (2)	1.4 (1)	6.8 (15)	–	4.2 (6)	0.4 (2)	0.4 (4)
Other prey	**6.1 (58)**	**6.4 (16)**	**4.1 (52)**	**6.2 (21)**	**6.6 (28)**	**8.5 (20)**	**3.6 (20)**	**2.5 (9)**
Thysanoessa spp.	–	1.6 (2)	–	1.0 (3)	–	2.8 (4)	–	–
Harpacticoid copepods	<0.1 (43)	–	<0.1 (26)	<0.1 (3)	<0.1 (7)	–	<0.1 (8)	–
Cyprids	<0.1 (42)	<0.1 (2)	<0.1 (32)	<0.1 (2)	<0.1 (2)	–	<0.1 (3)	–
Isopods	–	2.7 (4)	–	–	2.2 (4)	–	–	0.7 (1)
Nematodes	<0.1 (2)	–	<0.1 (1)	<0.1 (1)	<0.1 (4)	–	<0.1 (3)	–
Ostracods	<0.1 (10)	<0.1 (6)	<0.1 (16)	<0.1 (10)	<0.1 (12)	<0.1 (6)	<0.1 (6)	<0.1 (1)
Mollusk	3.3 (17)	1.3 (2)	2.4 (18)	1.4 (2)	2.3 (0)	0.2 (2)	2.3 (3)	–
All other	2.7 (13)	0.7 (2)	1.7 (8)	3.8 (6)	2.1 (2)	5.4 (9)	1.3 (4)	1.8 (6)
Unknown	**42.4 (58)**	**21.2 (31)**	**30 (47)**	**7.1 (25)**	**5.6 (12)**	**1.2 (17)**	**8.4 (18)**	**4.4 (13)**
Total number of prey	208	99	248	284	103	135	238	176
Total prey weight (g)	1.9	7.4	6.9	40.5	3.0	11.8	12.5	14.2
Total stomachs	60	51	74	115	57	55	90	68

Table 2.A-2 Arctic Staghorn Sculpin and Shorthorn Sculpin diets summarized by %MW and %O in two depth categories (≤30 m and >30m) of the west and east Beaufort Sea regions (WBS and EBS, respectively). Because "unknown" prey was common, it was included here. Total number of prey, total prey weight (g), and total stomachs are listed at the end of the table.

	WBS ≤30 m %MW (%O)		WBS >30 m %MW (%O)		EBS ≤30 m %MW (%O)	
Prey categories	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin	Arctic Staghorn Sculpin	Shorthorn Sculpin
Benthic amphipods	**29.7 (38)**	**15.9 (21)**	**24.0 (37)**	**6.4 (13)**	**21.0 (42)**	**8.4 (18)**
Anonyx spp.	2.5 (3)	–	0.5 (2)	–	–	–
Ischyocerus spp.	–	–	1.2 (1)	–	–	–
Melita spp.	1.9 (6)	0.3 (3)	6.9 (11)	3.8 (5)	4.0 (6)	–
Protomedeia spp.	3.6 (3)	–	1.3 (1)	–	4.5 (10)	–
Ampelescidae	–	–	0.1 (1)	–	0.6 (2)	–
Oedicerotidae	3.0 (3)	8.1 (10)	3.3 (8)	–	8.0 (16)	1.4 (5)
Unid. benthic amphipods	18.7 (29)	7.5 (10)	10.7 (22)	2.6 (10)	3.8 (24)	7.0 (18)
Calanoid copepods	**–**	**0.1 (3)**	**–**	**–**	**–**	**9.7 (18)**
Crabs	**13.0 (15)**	**23.3 (31)**	**6.9 (17)**	**14.4 (30)**	**–**	**13.3 (14)**
Chionocetes opilio zoea	–	–	–	<0.1 (3)	–	–
Paguridae juv.	–	8.2 (17)	4.3 (7)	10.4 (20)	–	3.8 (5)
Paguridae zoea	5.9 (9)	11.2 (14)	2.3 (6)	3.3 (15)	–	4.8 (5)
Unid. crabs	7.1 (6)	3.9 (7)	0.3 (4)	0.7 (10)	–	4.8 (5)
Cumaceans	**7.9 (18)**	**0.4 (3)**	**3.7 (9)**	**–**	**13.9 (22)**	**–**
Diastylidae	3.9 (9)	–	1.0 (2)	–	12.7 (22)	–
Leuconidae	0.1 (3)	–	0.3 (2)	–	–	–
Nannastacidae	–	–	1.1 (1)	–	–	–
Unid. cumaceans	3.8 (6)	0.4 (3)	1.3 (4)	–	1.2 (4)	–
Fish prey	**–**	**–**	**1.3 (1)**	**3.4 (5)**	**–**	**3.3 (5)**
Hyperiid amphipods	**–**	**39.3 (45)**	**1.3 (4)**	**71.0 (73)**	**1.8 (10)**	**29.1 (41)**
Hyperia spp.	–	–	0.2 (1)	0.2 (3)	1.7 (6)	1.0 (9)
Themisto libellula	–	28.0 (31)	1.1 (2)	55.8 (58)	–	22.5 (23)
Themisto spp.	–	11.1 (10)	<0.1 (1)	10.4 (13)	<0.1 (2)	4.1 (9)
Unid. hyperiid amphipods	–	0.1 (3)	–	4.6 (10)	0.1 (2)	1.4 (14)
Polychaetes	**22.2 (29)**	**0.9 (7)**	**22.5 (31)**	**2.5 (5)**	**37.2 (46)**	**10.8 (14)**
Flabelligeridae	3.4 (3)	–	–	–	–	–
Glyceridae	6.3 (9)	–	–	–	8.0 (8)	–
Phyllodocidae	–	–	0.1 (1)	–	–	–
Polynoidae	–	<0.1 (3)	–	–	4.1 (4)	–
Unid. polychaetes	12.4 (18)	0.9 (3)	22.4 (30)	2.5 (5)	25.0 (34)	10.8 (14)
Shrimps	**–**	**1.1 (7)**	**–**	**–**	**0.9 (2)**	**9.5 (9)**
Argis spp.	–	–	–	–	0.9 (2)	–
Crangonidae	–	0.3 (3)	–	–	–	–
Unid. Shrimps	–	0.8 (3)	–	–	–	9.5 (9)
Other prey	**3.5 (26)**	**7.6 (10)**	**2.0 (34)**	**2.4 (8)**	**1.6 (38)**	**0.2 (14)**
Thysanoessa spp.	–	–	–	2.2 (3)	1.6 (2)	–
Harpacticoid copepods	<0.1 (21)	–	<0.1 (8)	–	<0.1 (18)	<0.1 (5)
Cyprids	<0.1 (3)	–	<0.1 (24)	<0.1 (3)	<0.1 (6)	–
Isopods	2.6 (3)	0.2 (3)	–	0.2 (3)	–	–
Nematodes	–	3.7 (3)	<0.1 (1)	–	–	–
Ostracods	<0.1 (3)	–	<0.1 (3)	–	<0.1 (2)	<0.1 (5)
Mollusk	1.0 (12)	–	2.0 (6)	–	<0.1 (24)	0.2 (5)
All other	–	3.8 (7)	–	–	<0.1 (2)	–
Unknown	**23.8 (38)**	**11.4 (24)**	**38.3 (53)**	**<0.1 (3)**	**23.5 (46)**	**15.7 (27)**
Total number of prey	69	50	197	70	132	42
Total prey weight (g)	0.7	0.7	2.4	1.9	1.1	0.7
Total stomachs	34	29	90	40	50	22

Table 2.A-3 All prey taxa identified in the diets of Arctic Staghorn Sculpin and Shorthorn Sculpin in the SCS, NCS, WBS, and EBS. An "x" indicates presence in a species' diet.

	Arctic Staghorn Sculpin				Shorthorn Sculpin			
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**
Benthic amphipods	x	x	x	x	x	x	x	X
Ampeliscidae	x	x	x	x	x	x		
Ampelisca spp.	x				x	x		
Ampelisca eschrichti		x						
Ampelisca macrocephala	x	x				x		
Byblis spp.		x						
Byblis frigidus		x						
Haploops spp.				x				
Ampithoidae		x			x			
Ampithoe spp.		x			x			
Atylidae		x				x		
Atylus collingi		x				x		
Corophiidae	x	x	x	x	x	x		
Corophium spp.	x							
Pontoporeia spp.		x						
Protomedeia spp.	x	x	x	x	x	x		
Epimeriidae						x		
Paramphithoe spp.						x		
Eusiridae		x			x	x		
Rhachotropis spp.		x			x	x		
Isaeidae				x				X
Ischyroceridae	x	x	x		x	x		
Ericthonius spp.	x	x			x	x		
Ischyrocerus spp.		x	x		x	x		
Lysianassidae	x	x				x		
Orchomene spp.	x	x				x		
Maeridae		x			x	x		
Maera spp.		x			x	x		
Melitidae	x	x	x	x	x	x	x	X
Melita spp.	x	x	x	x	x	x	x	X
Oedicerotidae	x	x	x	x	x	x	x	X
Acanthostepheia spp.		x	x	x	x		x	X
Acanthostepheia behringiensis		x						
Acanthostepheia malmgreni		x						
Aceroides spp.	x	x	x		x	x		
Monoculoides spp.	x			x		x		X
Oediceros spp.	x				x			
Paroediceros spp.		x	x					X
Westwoodilla spp.					x			
Photidae	x	x				x		
Photis spp.	x	x				x		
Phoxocephalidae	x	x				x		
Grandifoxus spp.		x				x		
Harpina spp.	x	x						
Paraphoxus spp.		x				x		
Pleustidae						x		
Pleustes spp.						x		
Pontogeneiidae		x	x					
Pontogeneia spp.		x	x					
Stenothoidae	x				x			
Metopa spp.	x				x			
Synopiidae		x				x		
Syrrhoe spp.		x				x		
Uristidae	x	x	x	x	x	x		
Anonyx spp.	x	x	x	x	x	x		
Onisimus spp.	x							
Caprellid amphipod	x	x			x	x		

Table 2.A-3 continued Prey consumed by Arctic Staghorn Sculpin and Shorthorn Sculpin.

	Arctic Staghorn Sculpin				Shorthorn Sculpin			
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**
Calanoid copepods	**x**			**x**	**x**	**x**		**x**
Centropagidae	x							
Centropages abdominalis	x							
Metridinidae	x							
Metridia longa	x							
Euchaetidae								x
Euchaeta spp.								x
Calanidae	x	x			x	x	x	x
Calanus glacialis	x	x			x	x	x	x
Calanus hyperboreus				x				x
Neocalanus spp.						x		
Clausocalanidae	x							
Pseudocalanus spp.	x							
Crabs	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**
Decapoda (crab) zoea			x		x	x	x	x
Decapoda (crab) meg.		x			x	x	x	
Cheiragonidae	x	x			x	x		
Telmessus cheiragonus meg.	x				x			
Telmessus cheiragonus juv.	x	x			x	x		
Oregoniidae		x			x	x	x	
Chionoecetes opilio zoea					x	x	x	
Chionoecetes opilio meg.					x	x		
Chionoecetes opilio juv.					x	x	x	
Hyas coarctatus meg.		x			x	x		
*Hyas coarctatus*juv.		x			x	x		
Lithodidae					x			
Paralithodes spp.					x			
Paguridae	x	x	x		x	x	x	x
Paguridae zoea			x		x	x	x	x
Paguridae juvenile	x	x	x		x	x	x	x
Pagurus spp. juvenile		x						
Labidochirus splendescens						x		
Cumaceans	**x**	**x**	**x**	**x**	**x**	**x**	**x**	
Diastylidae	x	x	x	x	x	x		
Diastylis spp.	x	x	x	x	x	x		
Diastylopsis spp.				x				
Leptostylis spp.				x				
Leuconidae	x		x		x			
Eudorella spp.	x				x			
Eudorellopsis spp.	x							
Leucon nasica			x					
Nannastacidae	x		x		x	x		
Cumella spp.	x		x		x	x		
Euphausiids				**x**	**x**	**x**	**x**	
Euphausiidae				x	x	x	x	
Thysanoessa raschii				x	x	x	x	
Fish prey	**x**	**x**			**x**	**x**		
Agonidae					x			
Aspidophoroides olrikii					x			
Ammodytidae						x		
Ammodytes hexapterus						x		

Table 2.A-3 continued Prey consumed by Arctic Staghorn Sculpin and Shorthorn Sculpin.

	Arctic Staghorn Sculpin				Shorthorn Sculpin			
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**
Fish prey	**x**	**x**			**x**	**x**		
Cottidae	x				x	x		
Gymnocanthus tricuspis					x	x		
Gadidae						x		
Boreogadus saida						x		
Liparidae						x		
Liparis spp.						x		
Plueronectidae					x			
Stichaeidae	x				x	x		
Lumpenus fabricii					x			
Zoarcidae						x		
Gymnelus hemifasciatus						x		
Hyperiid amphipods	**x**		**x**	**x**	**x**	**x**	**x**	**x**
Hyperia spp.			x	x	x		x	x
Hyperia galba			x				x	
Hyperoche spp.							x	
Themisto spp.	x		x	x	x	x	x	x
Themisto abyssorum				x			x	x
Themisto libellula	x		x		x	x	x	x
Isopods		**x**	**x**		**x**	**x**	**x**	
Chaetiliidae			x					
Saduria spp.			x					
Idoteidae		x	x		x	x		
Synidotea spp.		x	x		x	x		
Mollusks	**x**	**x**	**x**	**x**	**x**	**x**		**x**
Bivalve	x	x	x	x	x	x		
Bivalve siphons	x							x
Gastropoda	x		x		x			
Carditidae		x						
Naticidae	x				x			
Lunatia pallida	x							
Nuculana spp.					x			
Pteropoda					x			
Trochidae					x			
Yoldiidae			x					
Polychaetes	**x**	**x**	**x**	**x**	**x**	**x**	**x**	
Ampharetidae		x						
Flabelligeridae			x					
Glyceridae			x	x	x			
Glycera spp.			x	x				
Goniadidae	x							
Glycinde spp.	x							
Lumbrineridae	x	x						
Lumbrineris spp.	x							
Maldanidae		x						
Nephtyidae	x	x						
Nephtys spp.	x	x						
Nuculidae	x							
Ennucula tenuis	x							
Oweniidae	x							
Phyllodocidae		x	x					
Phyllodoce groenlandica			x					
Polynoidae	x	x		x	x	x	x	
Arcteobia anticostiensis		x			x			
Gattyana spp.	x	x						
Harmothoe spp.		x			x	x		

Table 2.A-3 continued Prey consumed by Arctic Staghorn Sculpin and Shorthorn Sculpin.

	Arctic Staghorn Sculpin				Shorthorn Sculpin			
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**	**E Beaufort**
Polychaetes	**x**	**x**	**x**	**x**	**x**	**x**	**x**	
Hesperone adventor							**x**	
Terebellidae			x					
Shrimps	x	x		x	x	x	x	x
Crangonidae	x	x		x	x	x	x	
Argis spp.	x	x		x	x	x		
Crangon spp.						x		
Sclerocrangon boreas					x			
Hippolytidae					x	x		
Eualus spp.					x	x		
Pandalidae	x				x	x		
Pandalopsis spp.	x							
Pandalus spp.	x				x			
Other prey	x	x	x	x	x	x	x	x
Amphipoda frags	x	x	x	x	x	x	x	x
Bryozoa		x						
Copepod nauplii	x	x						
Cyclopoid copepod	x							
Cyprid	x	x	x	x	x		x	
Gastropod egg casing	x				x			
Harpacticoid copepod	x	x	x	x	x		x	x
Hydrozoa	x					x		
Ophiurodea		x				x		
Ostracoda	x	x	x	x	x	x		x
Tanaidacea		x			x			
Prey total	**89**	**88**	**54**	**42**	**101**	**98**	**36**	**31**

Table 2.A-4 Size distribution and descriptive information for all Arctic Staghorn Sculpin (Gt) and Shorthorn Sculpin (Ms) collected by PSBT and otter trawls over all cruises in the south Chukchi Sea (SCS), north Chukchi Sea (NCS), west Beaufort Sea (WBS), and east Beaufort Sea (EBS) regions.

	Chukchi Sea								Beaufort Sea					
	SCS ≤ 30 m		SCS > 30		NCS ≤ 30 m		NCS > 30 m		WBS ≤ 30 m		WBS > 30 m		EBS ≤ 30 m	
Summary information	Gt	Ms	Gt	Ms	Gt	Ms	Gt	Ms	Gt	Ms	Gt	Ms	Gt	Ms
Mean size (mm)	44.8	50.6	49.2	58.7	52.7	62.9	54.5	67.5	38.1	49.3	42.5	51.8	38.2	53.6
Min. size (mm)	28	31	28	33	25	31	31	36	25	36	28	42	25	31
Max. size (mm)	116	201	157	223	161	165	157	175	113	75	127	88	93	126
Std. Dev.	15.4	19.4	20.0	28.0	20.2	18.8	21.0	21.5	8.4	8.7	15.5	9.9	9.8	18.6
Sample size (n)	1495	1088	899	905	1159	686	1057	319	203	50	316	39	379	33

Appendix 2.B

Sculpin cumulative prey curves

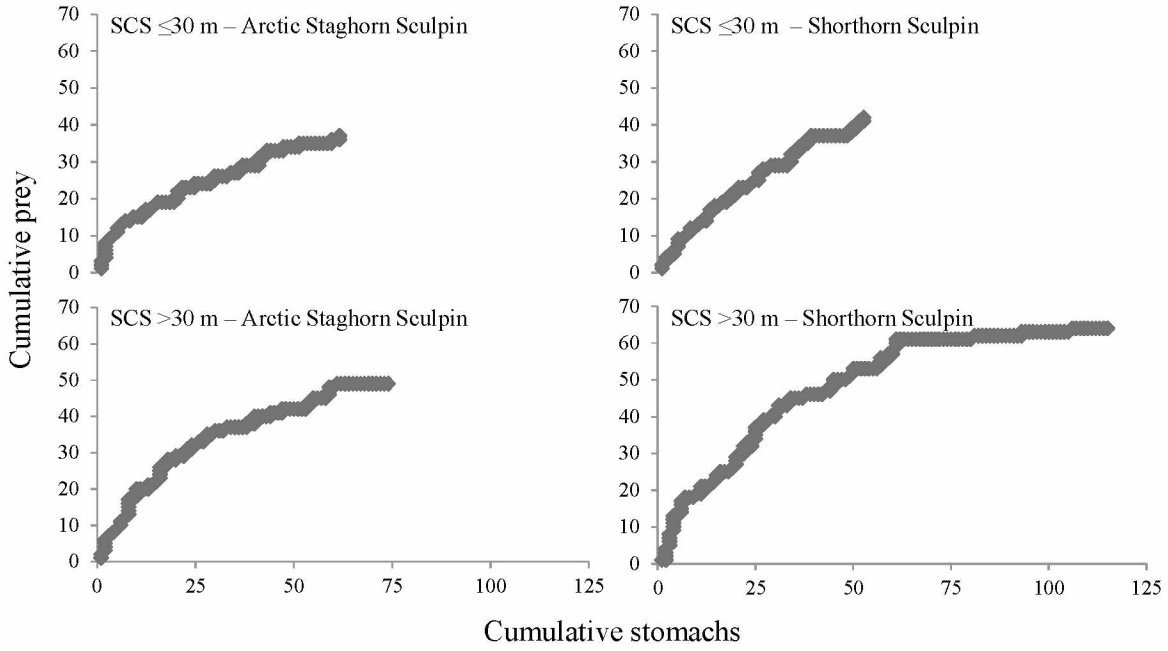

Fig. 2.B-1 Cumulative prey curves for Arctic Staghorn Sculpin and Shorthorn Sculpin in the south Chukchi Sea region (SCS).

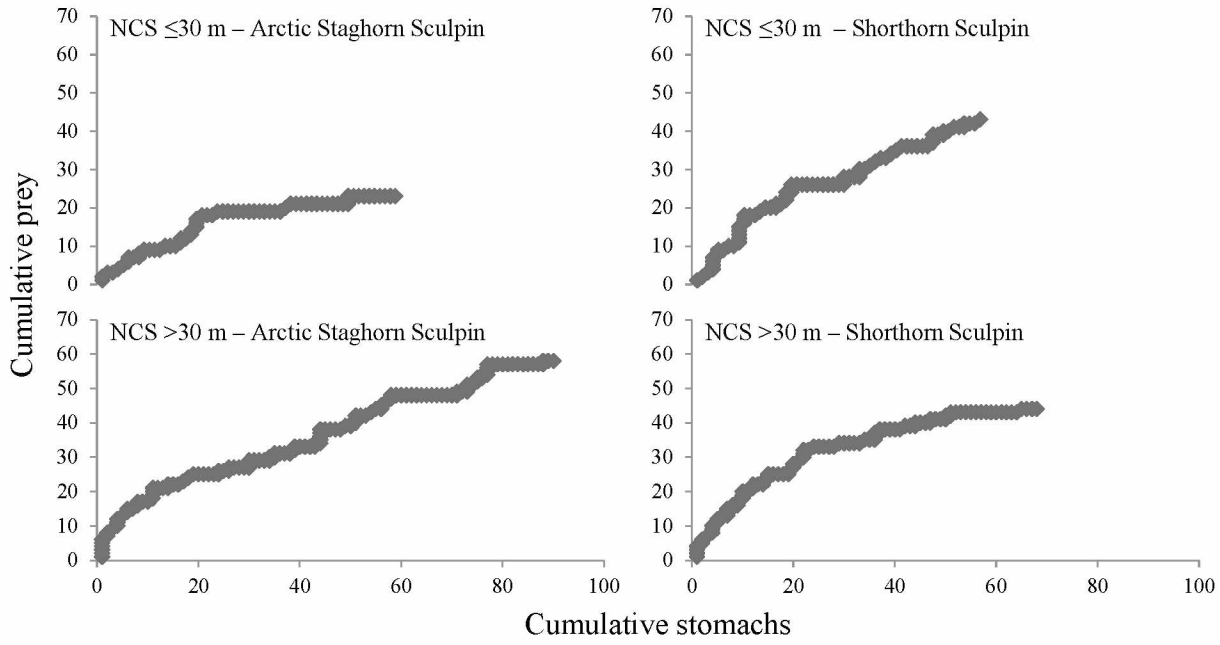

Fig. 2.B-2 Cumulative prey curves for Arctic Staghorn Sculpin and Shorthorn Sculpin in the north Chukchi Sea region (NCS).

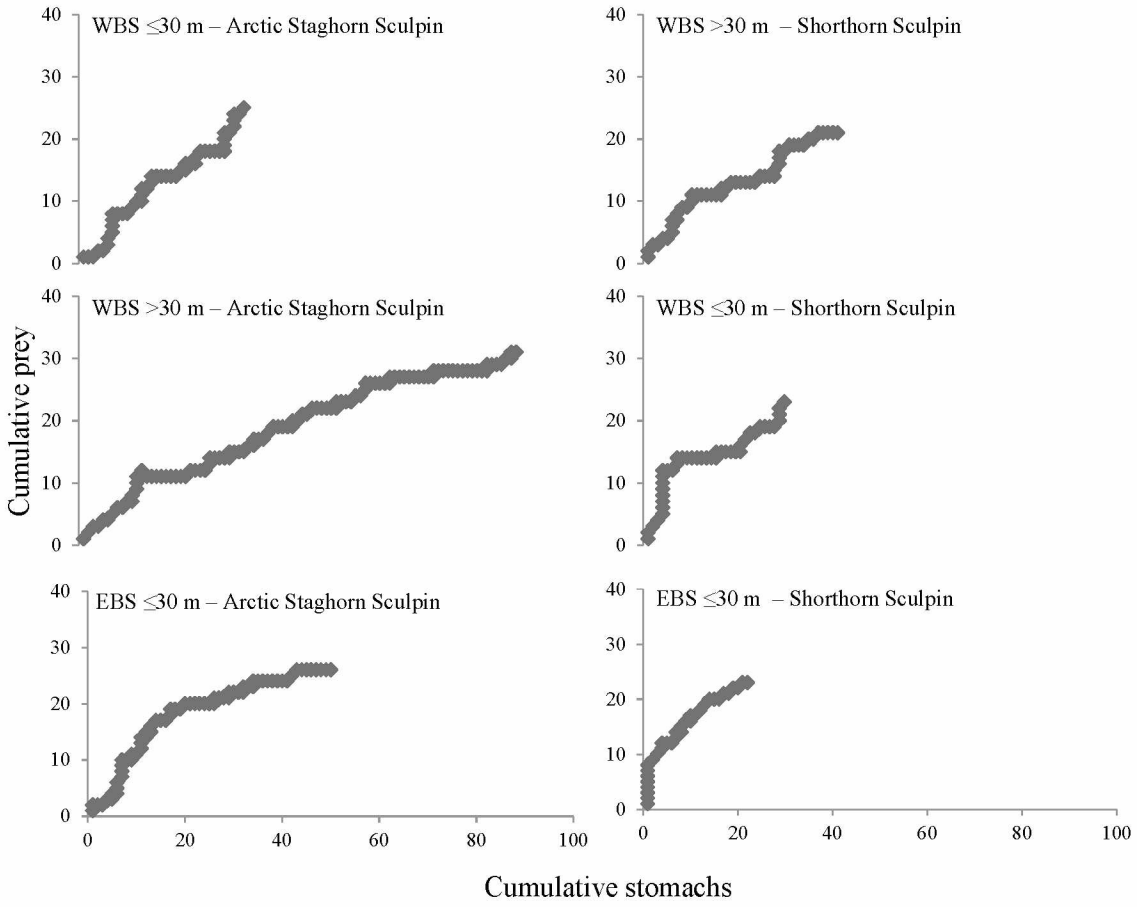

Fig. 2.B-3 Cumulative prey curves for Arctic Staghorn Sculpin and Shorthorn Sculpin in the west and east Beaufort Sea regions (WBS and EBS, respectively).

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Conclusions

The diet compositions of Arctic Cod, Arctic Staghorn Sculpin, and Shorthorn Sculpin differed substantially, yet the three species showed some similarities in their prey-use patterns throughout the Chukchi and Beaufort Seas. Each species consumed larger prey with increasing body size and consumed a higher diversity of benthic prey taxa in the Chukchi Sea than in the Beaufort Sea. This was an expected result because fishes commonly consume larger prey with an increase in body size (Labropoulou and Eleftheriou 1997) and because benthic productivity is characteristically higher in the Chukchi Sea (Grebmeier et al. 2006; Blanchard et al. 2013) compared to the Beaufort Sea (Carey and Ruff 1977; Carey 1987; Carey 1991). Interestingly, Shorthorn Sculpin followed a similar pattern to Arctic Cod in that both consumed proportionally more pelagic prey in the Beaufort Sea. I expected Shorthorn Sculpin to consume a predominantly benthic diet, regardless of body size, throughout both seas similar to Arctic Staghorn Sculpin. Instead, smaller, i.e., ≤60 mm, Shorthorn Sculpin in the Beaufort Sea consumed mostly pelagic prey such as hyperiid amphipods and crab zoea. It is not unheard of for sculpins to eat pelagic prey; the Ribbed Sculpin (*Triglops pingelli*) is known to consume pelagic zooplankton in the Canadian Beaufort Sea (Atkinson and Percy 1992). It is possible that both the Ribbed and Shorthorn Sculpin exhibit this type of feeding behavior as a means of resource partitioning as to not compete with other confamilial sculpins. In addition to meeting my objectives of documenting diet variability in each of these species' diets throughout the Chukchi and Beaufort Seas, I show that primarily benthic or pelagic fishes may feed similarly to one another in areas of high benthic or pelagic production. I would not have obtained these results without using habitat, i.e., sea, sea-region, or depth category, and body size as factors in my study.

I hypothesized that Arctic Cod diet would differ within and between the Chukchi and Beaufort Seas by four size classes, i.e., ≤50 mm, 51–70 mm, 71–100 mm, and ≥101 mm. My results mostly supported this hypothesis; however, there were some similarities. The diet of smaller Arctic Cod, i.e., ≤70 mm, was similar between the Chukchi and Beaufort Seas and consisted mainly of small (<5 mm) pelagic, calanoid copepods. This diet similarity is likely related to the prey handling constraints of smaller fishes (Werner and Gilliam 1984; Woodward and Hildrew 2002) and because smaller Arctic Cod (Quast 1974; Parker-Stetter et al. 2011; Walkusz et al. 2011) and their calanoid copepod prey (Auel and Hagen 2002) share similar vertical distributions throughout the water column and surface waters of various Arctic regions. Larger fish, (≥71 mm), within and between both seas consumed increasingly larger and more diverse prey taxa compared to smaller fish. Consistent with the differences between the more benthically productive Chukchi Sea and more pelagically productive Beaufort Sea, larger Chukchi Sea Arctic Cod consumed proportionally more benthic prey than Beaufort Sea conspecifics. This was expected because Arctic Cod can be bottom-associated in shallower Arctic regions (Bluhm and Gradinger 2008), such as the Chukchi Sea, which would make them more likely to consume benthic prey. This benthic feeding style has been documented in the relatively shallow eastern Bering Sea (Cui et al. 2012). Because of the connectivity of the Bering and Chukchi Seas, I believe larger Arctic Cod diet composition could reflect a gradient of benthic productivity, from high productivity in the Bering Sea to low in the Beaufort Sea. My research confirms that Arctic Cod is a generalist predator whose diet appears to reflect local prey availability (Renaud et al. 2012). Because Arctic Cod diet is not similar throughout the Arctic, its role in food webs probably differs depending on region inhabited.

Arctic Staghorn Sculpin and Shorthorn Sculpin diet compositions differed within all examined habitats, i.e., seas, sea-regions, and depth categories, and by species-specific mouth morphologies, which supported my sculpin diet hypotheses. I believe that sculpin body size confounded the effect of depth. Because of sample size limitations, it was not possible to test both body size and depth categories as covariates. Therefore, for these conclusions, I only focus on region and body-size-related results. Arctic Staghorn Sculpin and Shorthorn Sculpin showed the most diet similarities in the north Chukchi Sea, i.e., NCS region, where benthic amphipods occurred in 57–78% of their diets (Table 2.1). While a multitude of small-scale processes could be causing this similarity, two larger-scale processes that may have an effect are regional frontal boundaries (Weingartner 1997) and water circulation interacting with regional topographic features (Blanchard and Feder 2014), both of which could concentrate and deposit nutrients to the benthos within the NCS. The mouth gape morphology analyses explained why Arctic Staghorn Sculpin and Shorthorn Sculpin may be partitioning resources within habitats. Holding body length constant, Shorthorn Sculpin have significantly larger mouth gape width and height compared to Arctic Staghorn Sculpin, which allows them to eat larger prey. Because fish typically eat larger prey as they increase in body size to maximize energy gain (Werner and Gilliam 1984; Scharf et al. 2000), it follows that the larger-gaped Shorthorn Sculpin consume larger prey, e.g., crabs and fishes, while Arctic Staghorn Sculpin continue to consume relatively smaller prey, e.g., benthic amphipods and polychaetes. Additionally, the body size-based analysis indicated that at a similar size, Shorthorn Sculpin overlap Arctic Staghorn Sculpin in the size range of prey each can consume. Theoretically, Shorthorn Sculpin could consume a nearly identical diet as Arctic Staghorn Sculpin; however, their diets were very different. Both Sculpins

appear to be generalists that partition prey resources by taxa and size within shared habitats throughout the Chukchi and Beaufort Seas.

My results indicate that current Chukchi Sea food web model parameters should be updated with region-specific diet data and that future western Arctic food web models account for at least region- and size-specific differences in fishes' diets. Because diet composition data are limited for Chukchi Sea fishes, diet information from Bering Sea studies is used as a proxy in the Chukchi Sea model (Whitehouse 2013). That model parameterizes Arctic Cod diet composition as follows: 23% benthic amphipods, 17% copepods, 48% other zooplankton, 6% miscellaneous crustaceans, 2% shrimps, with the remaining 2% made up of fishes, bivalves, miscellaneous crabs, and polychaetes (Whitehouse 2013). Comparing the diet composition used in the model with my results (Table 1.1) shows that applying these Arctic Cod diet parameters would underestimate the importance of calanoid copepods and hyperiid amphipods in both seas, and overestimate the amount of benthic amphipods eaten by fish in the Beaufort Sea. Arctic Staghorn Sculpin diet composition in my study (Tables 2.A-1; 2.A-2) was quite similar to that used in the model, which was parameterized with benthic amphipods and polychaetes composing >80% of the diet composition. This suggests that Arctic Staghorn Sculpin diet could be similar throughout the Arctic and that using proxy diet composition could adequately model this species' feeding habits. Diet composition of Shorthorn Sculpin in the present research (Tables 2.A-1; 2.A-2) did not agree as well with the data used in the model. Shorthorn Sculpin in the Bering Sea was characterized as a heavy consumer (>80% of diet composition) of Snow Crab (*Chionocetes opilio*) and other crabs, with shrimps and benthic amphipods composing ~2.5 to 4% of the diet (Whitehouse 2013). This model overemphasizes the importance of snow crabs and other crabs, and undervalues the importance of shrimps, benthic amphipods, and hyperiid amphipods

consumed by Shorthorn Sculpin in the Chukchi Sea and would do the same for Beaufort Sea conspecifics. Therefore, to adequately model the effects of Shorthorn Sculpin on prey populations, both the benthic and pelagic components of its diet should be considered. These results show strong evidence that this and future diet comparison studies could enhance current and future modeling efforts by offering region and body size-specific diet data.

Climate change and resource development have the potential to alter present relationships between fishes and their prey in the Arctic. An increase in water temperature and decrease in sea ice is expected to facilitate a shift from benthic to pelagic-dominated food webs in areas throughout the Arctic (Grebmeier 2012). Additionally, oil well drilling will release sediments that could decrease benthic productivity in surrounding regions (Theil 2003). Oil spills directly and negatively affect fish and their prey resources (Peterson et al. 2003). My analyses indicate that the food habits of Arctic Cod and Shorthorn Sculpin are more flexible than that of Arctic Staghorn Sculpin. This flexibility might allow Arctic Cod and Shorthorn Sculpin to shift their feeding efforts depending on prey availability which would make them more adaptive to potential changes. I believe Arctic Staghorn Sculpin are primarily benthivores and that it and other benthic species would be the most affected by a shift towards a more pelagic food web or an oil spill. Therefore, as conditions shift, the ability of a species to adapt its food habits will likely be of great importance.

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Appendix
IACUC Approval

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Institutional Animal Care and Use Committee
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June 24, 2014

To: Brenda Norcross, Ph.D.
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [134765-15] Offshore fisheries surveys in the Chukchi and Beaufort Seas

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received:	June 18, 2014
Approval Date:	June 24, 2014
Initial Approval Date:	December 18, 2007
Expiration Date:	December 18, 2014

This action is included on the July 10, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*